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Systematics and diversification patterns of morphologically and ecologically diverse lineages of Agaricomycetes: Clavariaceae and Cantharellales

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I am submitting herewith a dissertation written by Joshua Mark Birkebak entitled "Systematics and diversification patterns of morphologically and ecologically diverse lineages of Agaricomycetes: Clavariaceae and Cantharellales." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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Systematics and diversification patterns of morphologically and ecologically diverse lineages of Agaricomycetes: Clavariaceae and Cantharellales

A Dissertation Presented for the
Doctor of Philosophy
Degree
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Joshua Mark Birkebak
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DEDICATION

I would like to dedicate this work to my parents Doug and Tambra Birkebak, the best research assistants I have ever had. While some parents may try to dissuade their 12 year old from pursuing mycological endeavors, they not only tolerated it but sacrificed so much time and energy encouraging my fascination. Without their support I never would have made it this far.

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ABSTRACT

The recent advent of molecular tools and methods to understand the diversity of living organisms allows for exploration of former untestable theories concerning the diversity of fungi. Here we assess the morphologically based classification of the family Clavariaceae in light of molecular phylogenetic reconstruction and propose a revised classification based on natural assemblages. We used stable isotope ratios to uncover a biotrophic nutritional mode for much of the family, which had not been well understood previously. Several enigmatic lineages of agaricoid and cantharelloid fungi within a clade of otherwise clavarioid fruiting bodies are also investigated. The first (partial) support for the Corner hypothesis of morphological evolution is provided. Up to three independent transitions to agaricoid clades and one transition to a cantharelloid clade were uncovered. A new generic classification for agaricoid clades including the discovery of a new genus and species is presented. Finally the effects of morphology and ecology on diversification rates are examined to explore which traits drive patterns of diversity found in the Agaricomycetes. Bayesian Analysis of Macroevolutionary Mixtures (BAMM) and State Speciation and Extinction (BiSSE and MuSSE) analyses were performed on time-calibrated phylogenies of two morphologically and ecologically diverse lineages (the Clavariaceae and the Cantharellales) to test hypotheses that changes in nutritional mode, fruiting body morphology, and hymenophore are associated with shifts in diversification rate. We find that a biotrophic nutritional mode is consistently associated with increased diversification rates while fruiting body morphology and hymenophore are only associated with shifts in the Cantharellales.

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INTRODUCTION

The great taxonomic, ecological, and morphological diversity of fungi has astounded and fascinated biologists for centuries. The revolution in molecular biology now provides insights into question that historically would have been considered unanswerable. Questions concerning taxonomic relationships, morphological evolution, and patterns of diversification rates, which were all once relegated to the realm of speculation and argumentation, are explicitly tested in the following chapters using the family Clavariacaeae and the order Cantharellales.

The first chapter seeks to test competing taxonomic arrangements proposed for the family Clavariaceae, elucidate the unknown trophic status of the family, and identify ancestral states and synapomorphies for different lineages. The familial composition and delimitation of genera had been contentiously debated and no universally consistent system was employed. Molecular phylogenetic methods are used to reconstruct natural relationships and revise taxonomic relationships. Stable isotope ratios of carbon and nitrogen are used to shed light on the unknown nutritional mode of the family. Ancestral state reconstruction is performed on the phylogenetic reconstructions to trace historical character evolution and discover synapomorphic characters.

The second chapter looks to further explore a specific lineage in the Clavariaceae that was found to contain several agaricoid (pileate lamellate) and cantharelloid (pileate non-lamellate) clades nested within an otherwise predominately clavarioid (non-pileate non-lamellate) family. An ancestral state reconstruction was performed on a multilocus phylogenetic reconstruction to trace character history and infer number and direction of morphological transitions. This is particularly interesting as the Corner hypothesis suggests that agaricoid lineages are derived from clavarioid lineages with cantharelloid intermediates. The effect of transitions in fruiting body morphology is assessed using two different Bayes inference methods and no significant affect on diversification rate was found.

The third chapter seeks to further explore and expand upon the findings concerning the effects of ecology and morphology on diversification rates. This is explored in two different groups with a high degree of ecological, fruiting body, and hymenophore diversity: the family Clavariaceae and the order Cantharellales. Multilocus time-calibrated molecular phylogenetic reconstructions are constructed for each clade. Bayesian inference is utilized to identify trait-specific diversification rates as well as locations of shifts in diversification rate along the phylogeny.

These chapters combined will increase our understanding of the evolution of fruiting body morphology and ecology in the Agaricomycetes. These analyses will provide an example of how to test for associations between traits and diversification rates and serve as a point of comparison for future studies.

CHAPTER I
A SYSTEMATIC, MORPHOLOGICAL AND ECOLOGICAL OVERVIEW OF THE CLAVARIACEAE (AGARICALES)

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The dissertation writer performed the majority of the lab work, performed the phylogenetic analyses, and was the primary author of the manuscript.

Abstract

The Clavariaceae is a diverse family of mushroom-forming fungi composed of species that produce simple clubs, coralloid, lamellate-stipitate, hydnoid and resupinate sporocarps. Here we present a systematic and ecological overview of the Clavariaceae based on phylogenetic analysis of sequences of the nuclear large subunit ribosomal RNA (nLSU), including nine from type collections. Forty-seven sequences from sporocarps of diverse taxa across the Clavariaceae were merged with 243 environmental sequences from GenBank and analyzed phylogenetically to determine major clades within the family. Four major clades or lineages were recovered: (i) *Mucronella*, (ii) *Ramariopsis*-*Clavulinopsis*, (iii) *Hyphodontiella* and (iv) *Clavaria*-*Camarophyllopsis*-*Clavicorona*. *Clavaria* is paraphyletic, within which the lamellate and pileate-stipitate genus *Camarophyllopsis* is derived and composed of two independent lineages. The monotypic genus *Clavicorona* also appears nested within *Clavaria*. The monophyly of *Clavaria* and Camarophyllopsis, however, cannot be statistically rejected. We compared differing classification schemes for the genera *Ramariopsis* and *Clavulinopsis*, most of which are inconsistent with the molecular phylogeny and are statistically rejected. *Scytinopogon*, a genus classified in the Clavariaceae by several authors, shares phylogenetic affinities with the Trechisporales. Overall 126 molecular operational taxonomic units can be recognized in the Clavariaceae, roughly half of which are known only from environmental sequences, an estimate that exceeds the known number of species in the family. Stable isotope ratios of carbon and nitrogen were measured from specimens representing most major phylogenetic lineages to predict trophic strategies. These results suggest that most non-lignicolous species feature a biotrophic mode of nutrition. Ancestral state reconstruction analysis highlights the taxonomic significance of at least nine morphological traits at various depths in the family tree.

Introduction

Figure 1. Diversity of sporocarp form in the Clavariaceae. Scale bar = 1 cm. 1.1 *Clavaria rubicundula*. 1.2. *Camarophyllopsis hymenocephala*. 1.3. *Mucronella bresadolae*. 1.4. *Ramariopsis* aff. *kunzei*. 1.5. *Ramariopsis fusiformis*. (Figures 1.1, 1.3, 1.4, 1.5 used with permission from Michael Wood; Figure 1.2 used with permission from D. Jean Lodge.)

Members of the Clavariaceae (Agaricales) produce a wide variety of sporocarp structures including pendant-hydnoid, cylindrical, clavate, coralloid, resupinate, and lamellate-stipitate sporocarps (Figs. 1). When first employed the genus *Clavaria* Vaill. ex L. and subsequently the family Clavariaceae Chevall. included mostly fleshy club- to coral-shaped fungi and eventually was placed in the highly polyphyletic order Aphyllophorales Rea (Rea 1922). Approximately 80 generic names have been associated with the Clavariaceae (Donk 1964), but the family has been gradually pruned of many genera and species, creating a more natural assemblage of taxa (viz. Corner 1950).

The Clavariaceae was first shown to have affinities with the Agaricales by Pine et al. (1999) using nuclear and mitochondrial ribosomal RNA loci but with few species sampled. The combination of *Clavaria*, *Clavulinopsis* Overeem and *Mucronella* Fr. later was indicated as a monophyletic group by Larrson et al. (2004). Dentinger and McLaughlin (2006) included the type of *Clavulinopsis* (Cu. sulcata Overeem) in their phylogenetic analysis and recovered a highly supported, monophyletic Clavariaceae including *Clavaria*, *Ramariopsis* (Donk) Corner, and *Mucronella*. Matheny et al. (2006) demonstrated that the pileatelamellate genus *Camarophyllopsis* Herink belonged in the Clavariaceae instead of the Hygrophoraceae Lotsy as classified by Arnolds (1986), Boertmann (2002), and Hesler and Smith (1963). The resupinate wood-inhabiting genus

Hyphodontiella Å Strid was shown to belong in the Clavariaceae by Larsson (2007), increasing the number of genera in the family to six.

None of the previous phylogenetic studies integrated all six known genera in a comprehensive analysis, and intrafamilial relationships have yet to be assessed. Furthermore, relationships of the genera *Clavicorona* Doty sensu stricto (excluding *Artomyces* Jülich) and *Scytinopogon* Singer to the Clavariaceae have not been explored, both of which produce coralloid sporocarps superficially similar to species of Ramariopis and *Clavaria*. *Clavicorona* and *Scytinopogon* have been classified in the Clavariaceae historically, but alternative classifications have been suggested (Hydnodontaceae by Jülich 1981 or the ‘‘Thelephoroid-series’’ by Corner 1950). Taxonomic disagreements over the relationships among the genera *Clavaria*, *Clavulinopsis* and *Ramariopsis* have not been settled (Table 1). All discussion of *Clavaria* and *Clavulinopsis* sensu Corner exclude taxa removed and placed in *Multiclavula* R.H. Petersen (Petersen 1967). While Dentinger and McLaughlin (2006) provided insights into the usefulness of some morphological characters to identify natural assemblages of taxa, we seek to increase taxon sampling, including incorporation of numerous molecular sequence data from the environment, to provide a more inclusive overview of phylogenetic relationships within the Clavariaceae. Dense taxon sampling has been demonstrated to improve accuracy of phylogenetic estimates based on multiple lines of evidence (Heath et al. 2008).

The ecological or trophic status of members of the family is wrought with conflicting reports in the literature. The Clavariaceae has been reported as mycorrhizal (Trappe 1962; Seviour et al. 1973; Englander and Hull 1980; Burke et al. 2005, 2006), saprotrophic (Rinaldi et al. 2008, Tedersoo et al. 2010), or possibly with an unknown biotrophic nutritional mode (Tedersoo et al. 2010). Phylogenetic analysis of environmental samples combined with stable isotope analysis can provide strong support for or against a biotrophic strategy (Hobbie et al. 1999; Nilsson et al. 2005; Ryberg et al. 2008, 2009; Mayor et al. 2009; Seitzman et al. 2011). These tools have not been widely applied to members of the Clavariaceae (Griffith et al. 2002), especially to species from forested habitat.

Our research objectives were to (i) reconstruct a molecular phylogeny of the Clavariaceae blending nLSU sequences from specimen vouchers with those recovered from the environment, (ii) perform ancestral state reconstructions on morphological characters used in Clavariaceae taxonomy and highlight characters consistent with recovery of clades at various phylogenetic depths, and (iii) predict trophic strategies across the family based on analysis of C and N stable isotope signatures and unidentified environmental sequences.

Table 1. A comparison of different classifications proposed by Corner (1950, 1970), Petersen (1978), and Jülich (1985) for the genera *Clavaria*, *Clavulinopsis*, and *Ramariopsis*. *The spores of *Clavulinopsis helvola* (Pers.: Fr.) Corner are considered smooth based on Pegler and Young (1985).

Taxon	Type species	Family	Tramal clamps	Spore ornamentation	Apiculus	Carotenes	Post meiotic mitosis
Clavaria Valliant ex L.: Fr. sensu Petersen	*Clavaria fragilis* Holmsk.: Fr.	Clavariaceae	+/-	Smooth/echinulate	Small-large	+/?	+/?
Clavaria Valliant ex L.: Fr. sensu Corner (=*Clavaria*, subg. *Clavaria* sensu Petersen)	*Clavaria fragilis* Holmsk.: Fr.	Clavariaceae	-	Smooth/echinulate	Small-large	?	?
Clavulinopsis Overeem sensu Corner	*Clavulinopsis sulcata* Overeem	Clavariaceae	+	Smooth*	Small-large	+/-	+/-
Clavaria subgenus *Clavulinopsis* (Overreem) R.H. Petersen	*Clavulinopsis sulcata* Overeem	Clavariaceae	+	Smooth	Small	+	-
Clavulinopsis Overeem sensu Jülich	*Clavulinopsis sulcata* Overeem	Clavariaceae	+	Smooth/roughened	Small-large	+/-	+/-
Ramariopsis (Donk) Corner sensu Corner	*Ramariopsis kunzei* (Fr.) Corner	Clavariaceae	+	Roughened	Large	-	+
Ramariopsis (Donk) Corner sensu Petersen	*Ramariopsis kunzei* (Fr.) Corner	Gomphaceae	+	Smooth/roughened	Large	-	+
Ramariopsis (Donk) Corner sensu Petersen, subg. *Ramariopsis*	*Ramariopsis kunzei* (Fr.) Corner	Gomphaceae	+	Roughened	Large	-	+
Ramariopsis, subg. *Laevispora* R.H. Petersen	*Ramariopsis minutula* (Bourdot & Galzin) R.H. Peteresen	Gomphaceae	+	Roughened under SEM	Large	-	+
Ramariopsis subg. *Donkella* (Doty) Petersen	*Ramariopsis corniculata* (Schaeff.: Fr.) R.H. Petersen	Gomphaceae	+	Smooth	Large	-	+

Materials and Methods

Taxon sampling

Effort was made to sample from diverse taxonomically recognized groups, including where possible representatives of generic and subgeneric nomenclatural types. While many species of Clavariaceae occur or are known only from the tropics, our sampling strategy relied primarily on specimens collected in the north and south temperate zones. Nine taxonomic type specimens deposited at TENN (herbarium abbreviations per Thiers [continuously updated]) were specifically targeted for sequencing. Morphological characters are provided for specimens examined by the authors or are taken from the literature (e.g. Corner 1950, Petersen 1988) for sequences deposited in GenBank.

Sequences from environmental samples can be informative in ecological and phylogenetic contexts (Ryberg et al. 2008, Nilsson et al. 2011). All fungal nuclear large subunit ribosomal RNA sequences (nLSU) were downloaded from GenBank (Benson et al. 2011) in Apr 2011 to glean sequences with affinities to the Clavariaceae. Insufficiently identified sequences (IIS) were separated from fully identified sequences (FIS) according to criteria used by the web tool emerencia (www.emerencia.org; Nilsson et al. 2005). Each IIS was compared for similarity with the FIS using BLAST (Altschul et al. 1990). A Perl script was used to parse from the BLAST output all IIS with a FIS belonging to *Camarophyllopsis*, *Clavaria*, *Clavicorona taxophila* (Thom) Doty, *Clavulinopsis*, *Hyphodontiella*, *Mucronella* and *Ramariopsis* as the most similar sequence. All sequences used for phylogenetic analysis in this study are included (Table 4 in appendix).

DNA extractions, PCR and sequencing

Dried tissue samples, 10–30 mg, were excised and ground in liquid nitrogen with a micropestle and sand in a 1.5 mL microtube. DNA extractions were performed with an E.Z.N.A.H Fungal DNA Kit (Omega Bio-Tek, Norcross, Georgia) for specimens fewer than 20 years old. A high performance kit, E.Z.N.A. HP Fungal DNA Kit (Omega Bio-Tek, Norcross, Georgia), was used on older specimens, particularly type specimens to reduce the degree of destructive sampling and increase chances of attaining PCR products. The isolated genomic DNA was diluted in two successive 1:10 sterile water solutions.

Primers pairs LR0R–LR7, LR0R–LR5, or LR0R–LR16 were used to amplify the 59– end of nLSU region on a Bio-Rad C1000 thermal cycler (Bio-Rad, Hercules, California). A mixture of sterile water and 53 buffer, GoTaq and dNTPs supplied by Invitrogen Corp. (Carlsbad, California) was prepared for each dilution of DNA and controls following manufacturer protocols. PCR conditions followed that of White et al. (1990). PCR products were viewed on a 1.0% agarose gel prepared with ethidium bromide and a UV transilluminator. Amplified LSU products were cleaned with a QIAquick PCR purification kit (QIAGEN, Valencia, California).

Sequence reactions were performed with a BigDye Terminator 3.1-cycle sequencing kit (Applied Biosystems, Foster City, California) and purified with Sephadex G-50 columns (General Electric Healthcare, Piscataway, New Jersey) using separator strips manufactured by Princeton Separations (Freehold, New Jersey). Sequencing was performed on an ABI 3730 48-capillary electrophoresis genetic analyzer at the Molecular Biology Resource Facility at the University of Tennessee. Sequence chromatograms were inspected and edited with Sequencher 4.9 software (Gene Codes Corp., Ann Arbor, Michigan).

Phylogenetic analyses

Forty-seven newly produced nLSU sequences were verified against potential contaminants in GenBank using BLAST (Altschul et al. 1990) and aligned with 33 sequences annotated as belonging to genera or clades of *Clavaria*ceae. We refer to this dataset as our initial alignment. A second alignment was created in CLUSTAL X (Larkin et al. 2007) to include 243 environmental sequences filtered as Clavariaceae by a BLAST procedure. *Anomoporia bombycina* (Fr.: Fr.) Pouzar, *Anomoporia kamtschatica* (Parmasto) Bondartseva, *Plicaturopsis crispa* (Pers.: Fr.) D.A. Reid and *Podoserpula pusio* (Berk.) D.A. Reid (Amylocorticiales Larrson, Binder & Hibbett) were used as outgroup taxa for both datasets based on Binder et al. (2010). Representative nLSU sequences of the Trechisporales K.H. Larss. from GenBank were aligned in CLUSTAL X with a sequence of *Scytinopogon angulisporus* (Pat. & Galliard) Corner and with two sequences of *Phlebiella* P. Karst. as outgroups. Minor adjustments to alignments were made in MacClade 4.08 (Maddison and Maddison 2005) as well as the removal of ambiguously aligned sites and a homologous group 1 intron that was present in some taxa in the Clavariaceae dataset. Alignments are available on TreeBASE (12414). jModelTest (Posada 2008) was used to determine the best-fit model of molecular evolution. Sequence data matrices then were analyzed by maximum likelihood (ML) with RAxML 7.2.3 (Stamatakis et al. 2008) with 1000 rapid ML bootstraps. The Shimodaira-Hasegawa test (SH test; Shimodaira and Hasegawa 1999) was performed in RAxML 7.2.3 (Stamatakis et al. 2008) on the dataset of vouchered specimens to test for monophyly of various topological constraints.

Ancestral state reconstruction (ASR) analyses

Maximum likelihood (ML) ancestral state reconstruction analyses were performed in Mesquite 2.75 (Madison 2011) with the Mk1 model on the ML tree produced from our initial alignment to determine potential synapomorphic traits in the *Clavaria*ceae. Eleven morphological and anatomical characters and character states were analyzed based on their importance stressed by systematic works (Corner 1950, Petersen 1978). Of these 11 characters, three are quantitative. To determine their states in a justifiable manner (Matheny and Kropp 2001), we calculated mean averages for each trait from 80 representatives in our phylogenetic analyses. Histograms were produced to examine the distribution of troughs in the data. These then were used as boundaries to

determine character states. If no troughs could be identified, we used the median value of the distribution as a boundary to establish two character states. Here are the 11 characters and states we considered: (i) trama clamp connections (present/absent); (ii) spore-wall chemistry (amyloid/inamyloid); (iii) basidia base (clamped/bifurcating/simple septate); (iv) size of basidia (23 µm, short; 23–38 µm, medium; 38 µm, long); (v) apicular prominence (small/medium/large); (vi) spore surface (smooth/echinulate/roughened); (vii) mean spore length (5.8 µm, short; 5.8 µm, long); (viii) mean spore shape (Q-value 1.29, globose to subglobose to broadly ellipsoid; Q= 1.29, elliptic to oblong); (ix) FeSO4 reaction to sporocarp tissue (negative/positive[green to blue-green]/ unknown); (x) color of sporocarps (white/gray/yellow/ orange/red/pink/purple); (xi) sporocarp morphology (simple/branched/agaricoid/resupinate/truncate/inflated/pendant).

Stable isotope analysis

To predict the likely nutritional mode of targeted fungal taxa in the Clavariaceae from every major lineage (excluding *Hyphodontiella*) and other taxa (see Table 5 in the appendix for specimens), we applied a discriminant multivariate analysis using fungal d15N and d13C isotope values and collector-based categorizations of nutritional mode (ECM vs. SAP) detailed in Mayor et al. (2009). Briefly, probabilities of categorical assignment were set proportional to occurrence and a pooled variance quadratic function was used because the assumption of equivalent covariance among variables was not met. In total, the discriminant model was ‘‘trained’’ using nutritional categorizations of 869 fungal sporocarp tissue samples previously published or detailed in Mayor et al. (2009) with the addition of a dataset containing archived *Ramaria* spp. from multiple, largely European, locations (Agerer et al. 2012).

Isotope analyses were conducted on ground and dried sporocarp tissue at the Smithsonian Tropical Research Institute’s mass spectrometry facility on a Flash 1112 Series Elemental Analyzer (Costech Analytical Technologies) coupled to a Delta V Advantage (Thermo Scientific) continuous flow (Finnigan Conflo III) isotope ratio mass spectrometer. Based on three internal standards, run error rates were 0.14%, and analytical error rates for four of the fungal species analyzed in triplicate had an average standard error of 0.06.

Results

Major clades and lineages of the Clavariaceae

A GTR+GAMMA+I model was selected as best fit to the initial nLSU alignment. The same model of molecular evolution was applied to the more taxonomically inclusive environmental dataset. No differences in topology of major clades were detected between analyses.

Clavariaceae is monophyletic including the genera *Camarophyllopsis*, *Clavaria*, *Clavicorona*, *Clavulinopsis*, *Hyphodontiella*, *Mucronella* and *Ramariopsis* (Figure 2). An nLSU sequence of *Scytinopogon angulisporus* yielded sequences with BLAST similarities most closely to species of

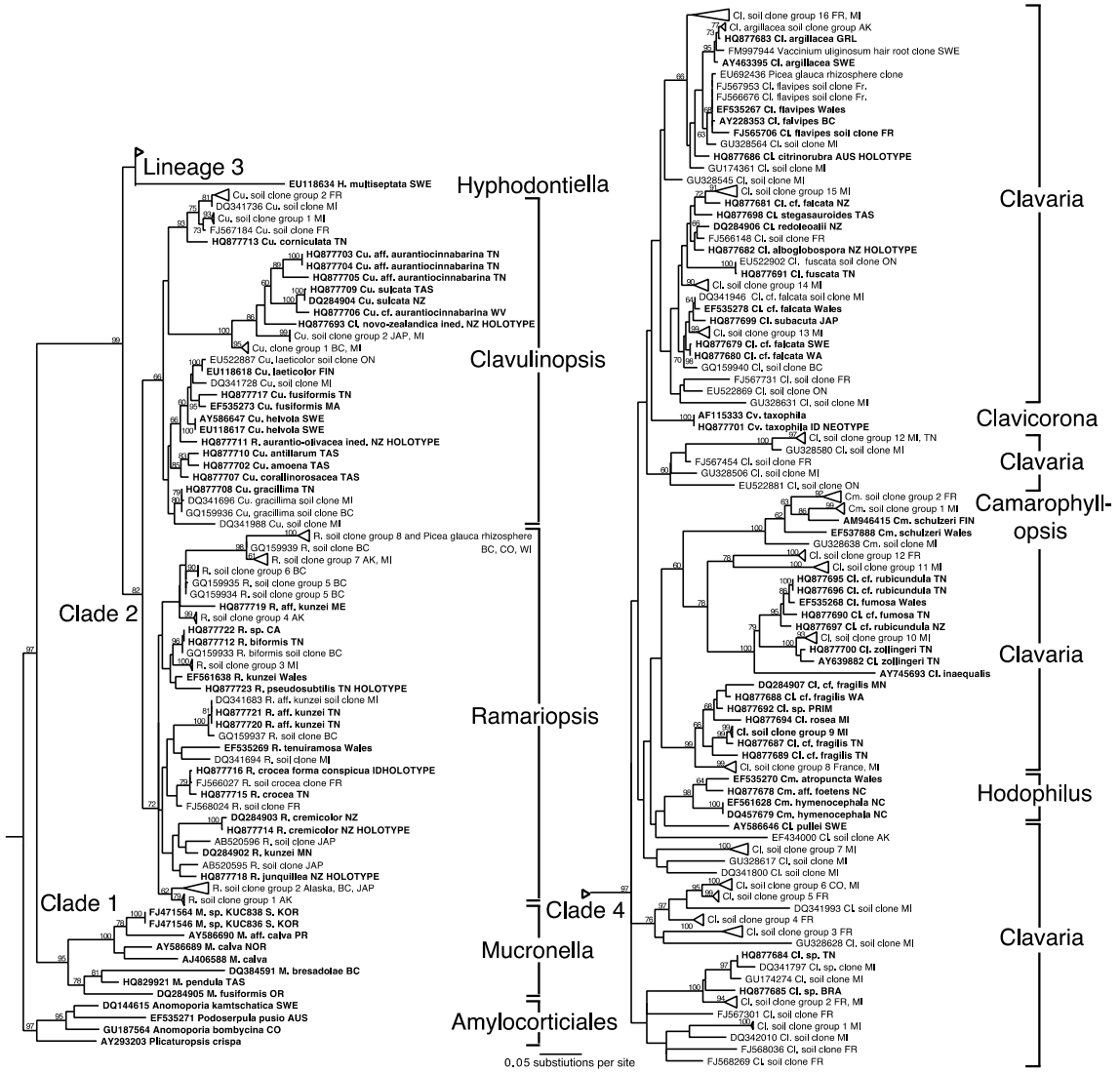

Figure 2. Maximum likelihood (ML) phylogeny of the Clavariaceae based on nLSU sequences from specimen vouchers and environmental data. Four major clades or lineages are identified and subdivisions indicated. Bootstrap values > 60% are indicated. Collapsed terminal groups (triangles) include redundant sequences. Four representative sequences of the Amylocorticiales are used for outgroup purposes.

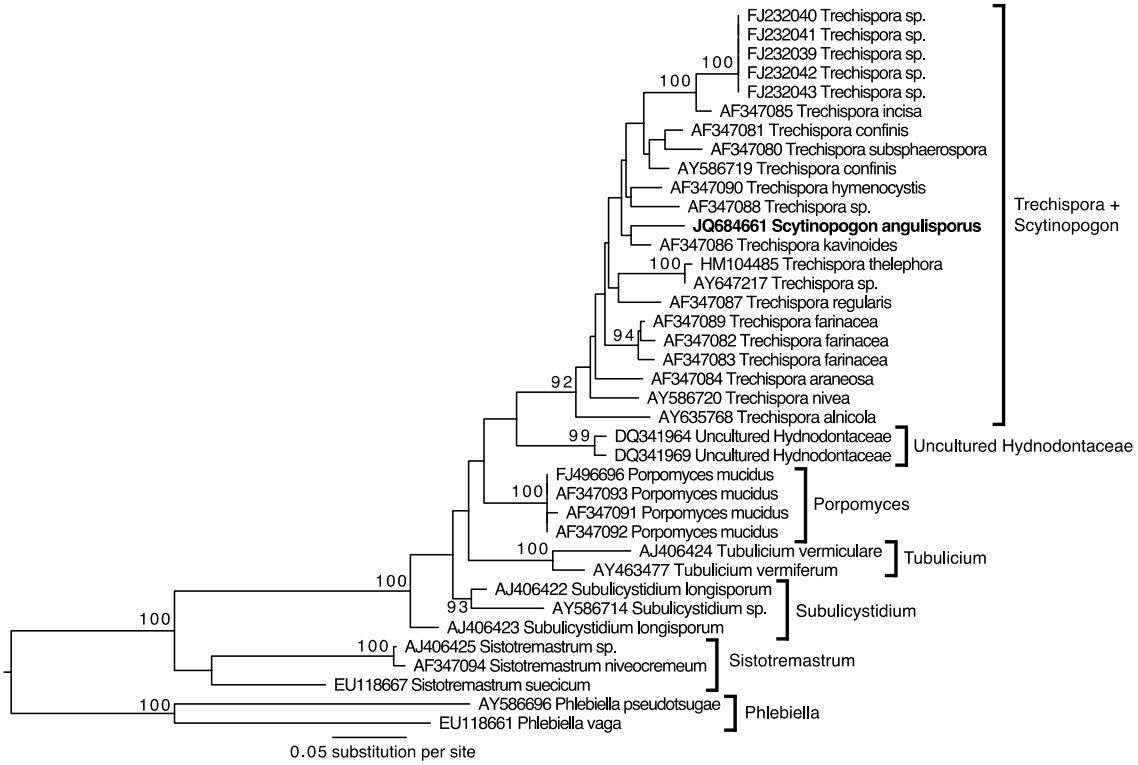

Figure 3. ML phylogeny showing the placement of *Scytinopogon* in the Trechisporales. Two species of *Phlebiella* are used for outgroup purposes. Bootstrap values > 60% are indicated.

Table 2. Classification and phylogenetic status of genera and subgenera of Clavariaceae. * denotes topologies that are significantly worse ($p < 0.05$) when constrained to be monophyletic and compared to the ML tree using the SH-test.**

Taxon	Phylogenetic status
Camarophyllopsis sensu Arnolds	polyphyletic
Camarophyllopsis sensu stricto	monophyletic
Clavaria sensu Corner 1950 (=*Clavaria* sensu Petersen excluding subg. *Clavulinopsis*)	paraphyletic
Clavaria sensu Petersen 1978	polyphyletic***
Clavaria subg. *Clavulinopsis*	polyphyletic
Clavicorona sensu stricto	single lineage
Clavulinopsis sensu Corner	polyphyletic***
Clavulinopsis sensu Jülich	monophyletic
Hodophilus	monophyletic
Hyphodontiella	single lineage
Mucronella	monophyletic
Ramariopsis sensu Corner	paraphyletic***
Ramariopsis sensu Petersen	paraphyletic***
Subg. *Donkella*	paraphyletic
Subg. *Laevispora* sensu Petersen 1966	polyphyletic***
Subg. *Laevispora* sensu Petersen 1988	polyphyletic***
Subg. *Ramariopsis*	paraphyletic*** (monophyletic if incl. subg. *Laevispora* sensu Petersen 1966)
Scytinopogon	Trechisporales (see also Larsson et al. 2011)

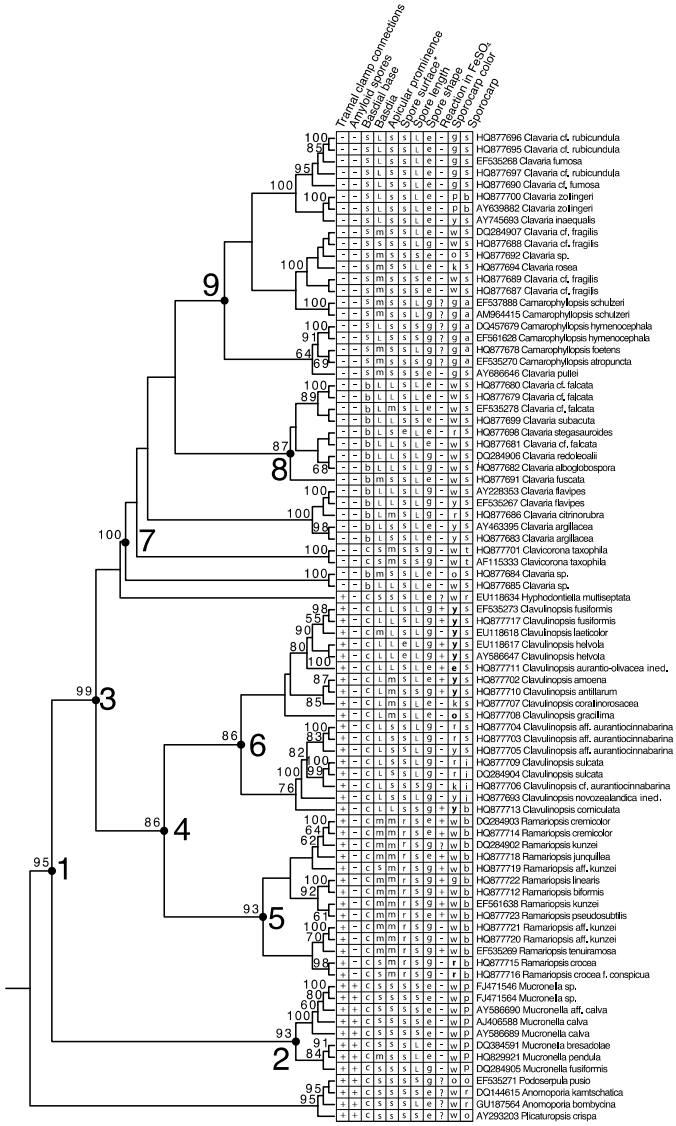

Figure 4. Phylogenetic distribution of morphological characters in the Clavariaceae according to a proportional branch length transformed ML phylogenetic reconstruction of sequences obtained from vouchered specimens. Key: clamp connections in trama, amyloidity and reaction in FeSO4, 2 (absent), + (present); basidial size and apicular prominence, s = small, m = medium, l = large; spore length, s = short, l = long; basidial base, b = bifurcate, c = clamped, s = simple septate; spore surface, e = echinulate, s = smooth, r = roughened (including those under SEM); spore shape, g = globose/ subglobose/broadly ellipsoid, e = ellipsoid/oblong; coloration of sporocarps g = gray, k = pink, o = orange, p = purple, r = red, w = white, y = yellow, boldface indicates retention of vivid coloration upon drying; basidiomata structure a = agaricoid, b = branched, i = inflated, o = other, p = pendant, r = resupinate, s = simple, t = truncate. (Numbered nodes are discussed in the text and correspond to TABLE 3.)

Trechisporales. A phylogenetic analysis of this dataset revealed *S. angulisporus* to be nested among 15 species of the genus *Trechispora* but with poor bootstrap support (Figure 3).

Four major well supported clades or lineages were recovered and are labeled clade 1 (*Mucronella*), clade 2 (*Clavulinopsis* + *Ramariopsis*), lineage 3 (*Hyphodontiella*, a single stem lineage) and clade 4 (including a paraphyletic *Clavaria*, a polyphyletic *Camarophyllopsis* and a single stem lineage *Clavicorona*) (Figure 2). One hundred twenty-six molecular operational taxonomic units (MOTUs) can be inferred from our analysis, 60 of which are composed solely of environmental samples. Only 10 MOTUs comprise sequences from both environmental and identified samples, and three represent plant root samples. Within clades 2 and 4 several robustly supported subclades were identified. Following the taxonomic scheme of Petersen (1978), *Ramariopsis* subgenus *Donkella* and *Clavaria* subgenus *Clavulinopsis* are paraphyletic and *Clavaria* is polyphyletic. The genus *Ramariopsis* sensu Petersen is paraphyletic. *Clavaria*, *Ramariopsis* and *Ramariopsis* subgenus *Laevispora* sensu Petersen all are rejected as monophyletic groups with the SH test (Table 2). According to classifications of Corner (1950, 1970), *Ramariopsis* is paraphyletic and *Clavulinopsis* is polyphyletic, both of which are strongly rejected as monophyletic entities by the SH-test (Table 2). *Clavicorona* is nested within *Clavaria*, and *Ramariopsis* subgenus *Laevispora* sensu Petersen is polyphyletic and nested within *Ramariopsis* sensu stricto. Details with respect to prior morphological-based classifications are presented in DISCUSSION.

Ancestral state reconstruction (ASR) analyses

Eleven morphological and anatomical traits were subjected to ASR analyses to determine potential synapomorphic traits in the Clavariaceae. (Node numbers refer those in Figure 4.)

The presence of tramal clamp connections (node 1) appears to be the ancestral condition in the Clavariaceae having been lost in the *Clavaria-Camarophyllopsis-Clavicorona* clade (clade 4 of Figure 2; Table 3). The basidial base is always clamped when clamps are present in the trama. The possession of clamped basidial bases, inamyloid spores and a non-resupinate habit unite clades *Clavuinopsis* and *Ramariopsis* at node 4 (clade 2 of Figure 2). It appears that the bifurcate basidial base, which is often interpreted as a wide, loop-like clamp connection, is associated with the loss of tramal clamp connections (node 7) except in *Clavicorona*. Simple-septate basidia and small apicular prominence may be morphological synapomorphies for a crown group of *Clavaria-Camarophyllopsis* species, but the node (9) uniting this group of taxa is weakly supported by nLSU molecular data. Medium basidial size, roughened spores, branched sporocarps and short spore length characterize members of clade *Ramariopsis* (node 5).

Amyloid spore walls and a pendant sporocarp morphology are unique to species of *Mucronella* (node 2). It is likely the most recent common ancestor of

the Clavariaceae featured amyloid spores. Inamyloid spore walls unite all other Clavariaceae (node 3). *Clavicorona taxophila* was reported by Dodd (1972) to have weakly amyloid spores, but Lickey et al. (2003) refuted this observation.

Echinulate-spored taxa have evolved more than once, but the roughened surface ornamentation found on spores of taxa of clade *Ramariopsis* (node 5) is a synapomorphic feature. Spore length was found to be informative for clade *Ramariopsis* (node 5), clade Holocoryne (node 8) and the previously mentioned crown group within *Clavaria* (node 9). Spore shape has little significant phylogenetic signal distinguishing only some smaller subclades of closely related tips. A positive reaction of sporocarp tissue to FeSO4 (ferric salts) likewise has little phylogenetic utility. Many sporocarp colors (white, yellow, orange, purple) can be found distributed across most major clades of Clavariaceae, but white is inferred as the ancestral color. The transition to yellow sporocarps is a likely synapomorphy for clade *Clavulinopsis* (node 6).

Although considerable plasticity is observed in sporocarp structure, a pendant type unites species of *Mucronella* (node 2), a branching type joins species of clade *Ramariopsis* and a simple type appears to be a synapomorphy for the *Clavaria-Camarophyllopsis-Clavicorona* clade (node 7). Agaricoid (lamellate and stipitate-pileate) species of *Camarophyllopsis* appear to have evolved twice in the *Clavaria-Camarophyllopsis-Clavicorona* clade. However, the monophyly of *Camarophyllopsis* cannot be rejected by nLSU data alone (Table 2).

Stable isotopes

The dual isotope values from Clavariaceae sampled here spanned much the range of that observed globally (Figure 5). Discriminant analysis provided strong support (e.g. >89–100%) for a biotrophic habit in all members of *Camarophyllopsis*, *Clavaria*, *Clavulinopsis* and *Ramariopsis*. The two *Mucronella* spp. and two *Clavicorona taxophila* collections were classified as saprotrophic with a greater than/equal to 99% probability (see Table 5 in the appendix). Of the remaining taxa analyzed, only *Galiella rufa* (Schwein.) Nannf. & Korf, *Dennisiomyces* sp. and *Marasmius fulvoferrugineus* Gilliam had nutritional predictions that were equivocal (e.g. <70%; Table 5 in the appendix). From our dataset, interspecific variability of ∂15N values was generally low in *Clavaria* cf. *fragilis* Holmsk.: Fr. (plus-or-minus SE) = 12.26 plus-or-minus 0.60% (two collections from Tennessee and one from California) but higher in three separate Tennessee collections of *Clavulinopsis fusiformis* (Sowerby: Fr.) Corner 5 16.95 plus-or-minus 1.87%.

Discussion

Familial compositions

Studies have delimited the Clavariaceae on a molecular basis (Matheny et al. 2006, Dentinger and McLaughlin 2008, Larrson 2008), but none provided an

Table 3. ML ancestral state reconstruction analysis results for eleven morphological characters of the Clavariaceae. Significant probabilities (*P* >0.95) are indicated by *. Other probability values are provided. All nodes are strongly supported with exception to node 9. Abbreviations the same as those used in Figure 4.**

Character	node 1	node 2	node 3	node 4	node 5	node 6	node 7	node 8	node 9
tramal clamps	+ ***	+ ***	+ ***	+ ***	+ ***	+ ***	- ***	- ***	- ***
amyloid spore walls	+ (.94)	+ ***	- ***	- ***	- ***	- ***	- ***	- ***	- ***
base of basidia	c ***	c ***	c ***	c ***	c ***	c ***	b (.80)	b ***	s ***
size of basidia	s (.49) m (.38)	s (.62) m (.32)	m (.64) l (.24)	m (.66) l (.28)	m ***	l ***	m (.70) l (.18)	l ***	m ***
apicular prominence	s (.88)	s ***	s (.61) m (.37)	m ***	m ***	m ***	s (.87)	l ***	s ***
spore surface	s ***	s ***	s ***	s ***	r ***	s ***	s ***	s ***	s ***
spore length	s (.42) l (.58)	s (.39) l (.61)	s (.42) l (.58)	s (.49) l (.51)	s ***	l (.90)	s (.20) l (.80)	l ***	s (.29) l (.71)
spore shape	g (.45) e (.55)	g (.36) e (.64)	g (.59) e (.41)	g (.65) e (.35)	g (.92)	g (.33) e (.67)	g (.61) e (.39)	g (.63) e (.37)	g (.56) e (.44)
$FeSO_4$ reaction	- (.92)	- ***	- (.75) + (.25)	- (.47) + (.53)	- (.38) + (.62)	- (.42) + (.58)	- ***	- ***	- ***
sporocarp color	w ***	w ***	w ***	w ***	w ***	y ***	w ***	w ***	w (.44) g (.56)
sporocarp morphology	p (.71) s (.18)	p ***	s (.81)	s (.78) b (.20)	b ***	s (.87)	s ***	s ***	s ***

inclusive systematic treatment of all known higher-level taxa, including generic and subgeneric representation or incorporated unidentified environmental samples. Our results indicate that the generic classification of Corner (1950) withthe modification proposed by Petersen (1966) (i.e. *Ramariopsis* subgenus *Laevispora*) but not Petersen (1978) (i.e. splitting *Clavulinopsis* into *Clavaria* subgenus *Clavulinopsis* and *Ramariopsis* subgenus *Donkella*) most accurately reflect the systematic relationships uncovered in this study. *Clavaria* is paraphyletic due to inclusion of *Clavicorona* and two lineages of *Camarophyllopsis* sensu Arnolds, but support is lacking along the backbone of clade 4 (Figure 2). If the two clades of *Camarophyllopsis* were treated as separate genera, one could be considered *Camarophyllopsis* sensu stricto (typified by *C. schulzeri* (Bres.) Herink) and the other a resurrected Hodophilus R. Heim (typified by C. foetens [W. Phillips] Arnolds). These results will require further verification with multigene data and increased taxon sampling because enforcing *Camarophyllopsis* sensu Arnolds as a monophyletic entity could not be rejected by the data at hand (Table 2).

Phylogenetic relationships

Here we report that the Clavariaceae includes the genera *Camarophyllopsis*, *Clavaria*, *Clavicorona*, *Clavulinopsis*, *Hyphodontiella*, *Mucronella* and *Ramariopsis*. *Scytinopogon* was found to cluster with *Trechispora* P. Karst. in the Trechisporales as was proposed by Jülich (1981) and not in the Clavariaceae as suggested by Corner (1950, 1970) and García-Sandoval et al. (2005).

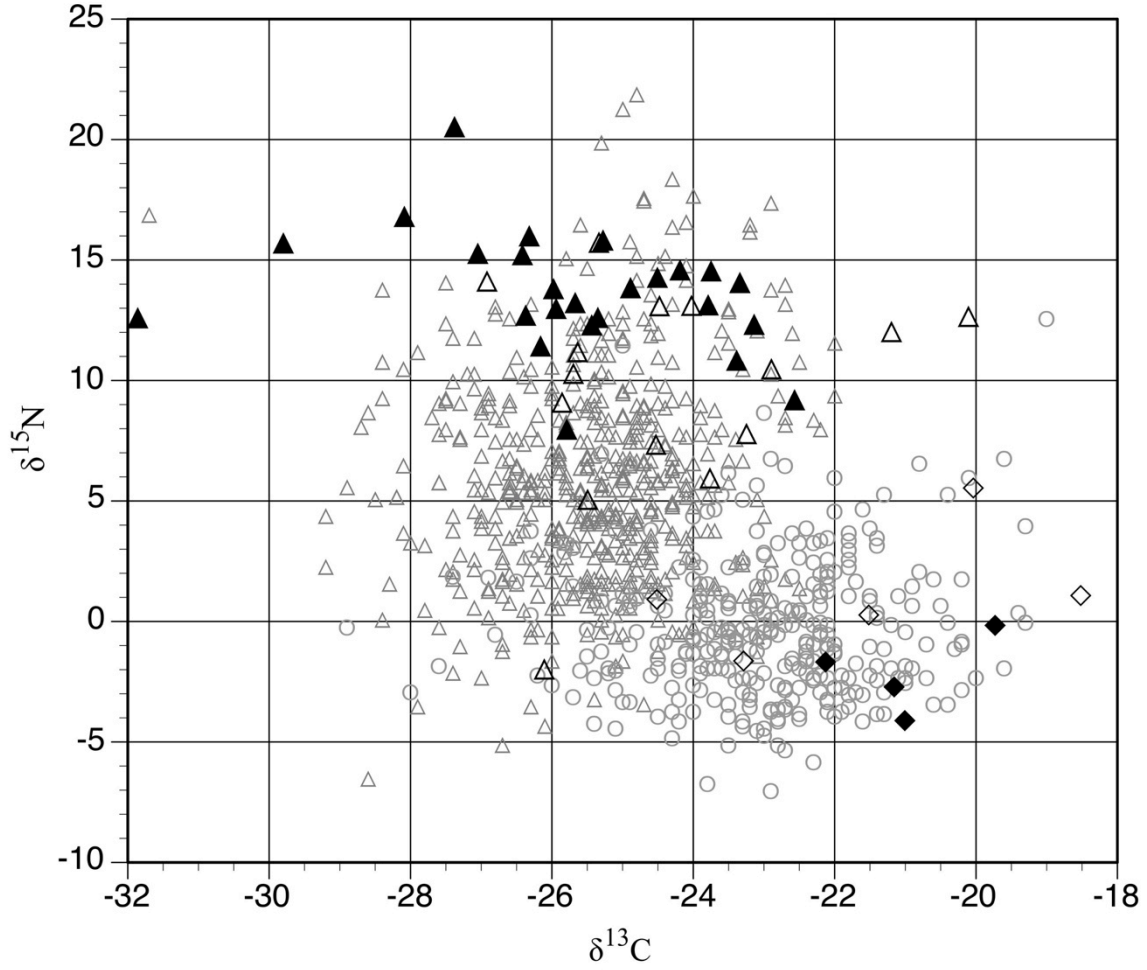

Figure 5. Isotope biplot illustrating placement of samples of Clavariaceae and other fungal basidiomata analyzed in this study within a global dataset of basidiomata isospace. Black-filled triangles are biotrophic-categorized Clavariaceae fungi, black hollow triangles are control ectomycorrhizal taxa, black-filled diamonds are saprotrophic (SAP) Clavariaceae fungi and black hollow diamonds are other control SAP taxa. In the background are biotrophic and ECM taxa as gray hollow triangles and SAP taxa as gray hollow circles used in a discriminant multivariate analysis of 869 collector-categorized sporocarps. This global dataset include values from Mayor et al. (2009) with the addition of Ramaria spp. from Agerer et al. (2012) and span sites from tropical, temperate, boreal and arctic biomes.

Mucronella is monophyletic and the sister group to the rest of the Clavariaceae. The phylogenetic position of the Clavariaceae overall is not known with confidence, but recent work suggests the family may be the sister group to the rest of the Agaricales (Binder et al. 2010). Our ASR analyses (Table 3) indicate no obvious morphological synapomorphies for the family with confidence despite high molecular support for recognition of the group by more taxonomically inclusive studies of Agaricales (Matheny et al. 2006, Binder et al. 2010). Nevertheless, the most recent common ancestor of the Clavariaceae may have produced white sporocarps, possessed clamps throughout the trama and on the bases of the basidia, and had smooth spores that were most likely to be amyloid (Table 3). Discussion of the four major clades or lineages of Clavariaceae recovered in this study follow below.

Clade 1. This clade contains the genus *Mucronella*, and its type species *M. calva* (Alb. & Schwein.) Fr. *Mucronella* is recovered as sister to the remainder of the Clavariaceae with high bootstrap support (Figures 2, 4). Larsson et al. (2004) were the first to indicate a phylogenetic relationship between *Mucronella* and other groups of Clavariaceae. The genus was thought to be allied with the Russulales due to it similarity to *Hericium* Pers., culturability and amyloid spores (Harrison 1972). Eight species are accepted worldwide (Kirk et al. 2008). Seven independent clades that would correspond to phylogenetic species were recovered here from eight sequences representing five morphospecies. Synapomorphies for the clade include the pendant or positively gravitropic sporocarps, lignicolous habit and ability to grow as mycelia in culture (Stebbins and Robbins 1949). The amyloidspored condition may be symplesiomorphic. In addition, the species in this clade have small basidia (10– 20 µm long) and clamped tramal elements. No environmental isolates corresponding to *Mucronella* were found in GenBank.

Clade 2. This strongly supported inclusive group (Figures 2, 4) contains clades *Ramariopsis* and *Clavulinopsis* and corresponds well with *Clavulinopsis* sensu Jülich (1985). The unique combination of clamped basidia, clamped tramal hyphae, inamyloid spores and non-resupinate habit (node 4, Figure 4) unites the group as a whole. Basidiomata of many taxa react with ferric salts, producing a green or blue coloration, but this is not a consistent character. *Ramariopsis* and *Clavulinopsis* sensu Corner (1970) are paraphyletic and polyphyletic respectively. *Ramariopsis* sensu Petersen (1978) is paraphyletic, and his *Clavaria* subgenus *Clavulinopsis* is polyphyletic.

Within clade 2, clade *Ramariopsis*, typified by *R. kunzei* (Fr.: Fr.) Corner, receives high bootstrap support. Morphological characters that unite clade *Ramariopsis* include species with medium basidia (ca. 23–38 µm long), short spores (mean, 5.8 µm long) with roughened surface ornamentation, medium apicular prominence and branched basidiomata. Nearly all are white to tan or pale yellow, and many species react to ferric salts. This clade corresponds to *Ramariopsis* sensu Corner (1970) plus species with spores that appear smooth under light microscopy he classified as *Clavulinopsis*, which Petersen (1966)

placed in *Ramariopsis* subg. *Laevispora*. Our results do not support Petersen's (1978, 1988) placement of subgenus *Laevispora* (typified by *R. minutula* [Bourdot & Galzin] R.H. Petersen) in synonymy with subgenus *Donkella* (typified by *Cu. corniculata*). Our data support the speculation of Pegler and Young (1985) that subgenus *Laevispora* does not delimit a natural assemblage of taxa and should be treated as a synonym of *Ramariopsis* subgenus *Ramariopsis*.

Sister to clade *Ramariopsis* is clade *Clavulinopsis*, typified by *Cu. sulcata* Overeem, which receives moderate to high bootstrap support (Figures 2, 4). Morphological characters indicative of members of clade *Clavulinopsis* include large basidia (mean, 38 µm long) and likely large spores (mean, 5.8 µm long) with smooth walls. Some taxa react to ferric salts on the surface of their sporocarps and produce spores with distinctly large apiculi. Other species of clade *Clavulinopsis* centered around *Cu. sulcata*, and the *Cu. aurantiocinnabarrina* group do not react to ferric salts and have spores with small apiculi. *Clavaria* subgenus *Clavulinopsis* in the sense of Petersen is paraphyletic due to the inclusion of *Ramariopsis* subgenus *Donkella* represented by *Cu. corniculata.*

Lineage 3. This lineage contains the only published sequence of the genus *Hyphodontiella*, typified by *H. multiseptata*. *Hyphodontiella* is unique to the Clavariaceae by virtue of its resupinate sporocarps. The hymenophore is smooth. *Hyphodontiella multiseptata* is described with small basidia (10–20 µm long), navicular spores that are non-reactive in Melzer's reagent and that feature small apiculi and clamped, frequently septate, tramal elements. The phylogenetic position of *H. multiseptata* is weak, but nLSU data suggest it may be the sister lineage to the *Clavaria*-*Camarophyllopsis*-*Clavicorona* assemblage. Based on the literature, a second species, *H. hauerslevii* K.H. Larss. & Hjortstam, is distinct in having large cystidia, non-clamped tramal elements and elongate elliptic spores (Hjortstam and Larsson 1995). Both species are known only from northern Europe. We suspect the genus may not be monophyletic given the presence of such conspicuous cystidia in *H. hauerslevii*.

Clade 4. This large inclusive group encompasses the genera *Clavaria*, *Camarophyllopsis* and *Clavicorona*. These three genera are recovered in a single clade with robust support (Figures 2, 4) within which there is little resolution along the backbone. Multigene studies will be necessary to add any additional phylogenetic resolution within clade 4. Nonetheless, this group of taxa contains a high diversity of morphological character combinations including species with pseudocystidia, tramal clamp connections and inflated, truncate sporocarps (*Clavicorona*); pileate-stipitate sporocarps with lamellae with or without tramal clamp connections (*Camarophyllopsis*); and taxa lacking tramal clamp connections, with or without bifurcate clamp connections at the base of the basidia and primarily club-shaped to cylindrical sporocarps (*Clavaria*). The spores may be smooth, echinulate or echinulate-punctate, but known species do not produce a green or blue reaction to ferric salts. To our knowledge species of *Camarophyllopsis* have not been tested for ferric salt reactions.

Clavaria sensu Corner traditionally was recognized to contain species with typically secondarily septate tramal elements always lacking clamp connections, simple-septate basidia or basidia with bifurcate clamp connections, and cylindrical, club-shaped or coralloid sporocarps. Despite the lack of resolution among more deeply branching nodes, we have recovered several well supported terminal subclades within clade 4 (Figure 4, nodes 8, 9, 10). Species that descend from node 8 (clade Holocoryne) are distinguished from other well supported groups by the presence of bifurcating basida. Species descending from nodes 9 (clade Clavaria) and 10 (clade fumosa) feature simple-septate basidia. *Clavaria*, however, appears to be paraphyletic, but its monophyly in the sense of Corner cannot be rejected (Table 2) given nLSU data only.

Members of *Camarophyllopsis* are polyphyletic and split into two well supported clades. Each clade may be defined by the structure of the pileipellis, but additional species remain to be sampled. No representatives of taxa with clamp connections have been sequenced (e.g. *Camarophyllopsis dennisiana* [Singer] Arnolds features clamp connections). Two separate evolutionary transitions to a pileate-stipitate sporocarp with lamellae are supported by our data, but the monophyly of *Camarophyllopsis* cannot be rejected presently (Table 2).

Clavicorona is a monotypic genus nested within *Clavaria* (clade 4) with strong bootstrap support (Figures 2, 4). The combination of the following traits distinguishes it from the rest of the Clavariaceae: presence of pseudocystidia, cristate truncate apices and the differentiation of hymenium from a sterile upper surface.

Corner (1950, 1970) and García-Sandoval et al. (2005) classified the genus *Scytinopogon* within the Clavariaceae based on sporocarp morphology and micromorphology. However, our results suggest that *Scytinopogon* clusters within the genus *Trechispora* in the Trechisporales (Figure 3). Although the type of the genus, *S. pallescens* (Pat.) Singer, has not been sampled, *S. angulispora* has been considered conspecific with *S. pallescens* by most authors (Corner 1950, Petersen 1988). A phylogenetic relationship between *Scytinopogon* and the Trechisporales was predicted by Jülich (1981) and also has been reported independently in a conference abstract by Larsson et al. (2011).

Saprotrophic and biotrophic nutritional modes in the Clavariaceae

Few studies have assessed the nutritional mode of species of Clavariaceae. However, those who have done so point to possible biotrophic associations with species of Ericaceae. A species in the *Clavaria fragilis* group has been shown to be directly associated with cortical root cells in *Rhododendron* using serological and morphological evidence (Seviour et al. 1973). *Clavaria argillacea* Pers.: Fr. has been shown to exchange nutrients with ericoid hosts using direct isotope application (Englander and Hull 1980).

Here we determined N- and C-stable isotope values to infer nutritional modes of samples of Clavariaceae. Globally biotrophic and ECM fungi have a

mean d15N and d13C value of 5.81 and 225.39%, whereas SAP fungi are 20.34 and 222.98% respectively (n = 869). In contrast, the taxa analyzed here had a mean d15N and d13C value of 12.2 and 225.20% respectively, and SAP fungi were close to global means (20.25 and 221.33 respectively). These relatively 15N-enriched sporocarp values encompass the upper 90th percentile of the global dataset used in this analysis (n = 869) and an additional dataset that also includes unpublished fungal isotope values (n = 1269). Such 15N-enriched sporocarp values, irrespective of the relatively less variable d13C values, are in part why the probabilities assigned to ECM fungi were consistently high (e.g. ~ 100%), suggesting a possible previously unknown biotrophic nutritional mode.

Multiple non-exclusive hypotheses for 15N enrichment in sporocarps have been posited. The most successful involves the cumulative retention of 15N during the synthesis and delivery of 15N-depleted transfer compounds to host plants in exchange for photosynthate (Hobbie and Hobbie 2006), thus justifying our discriminant-based categorizations. This model has the added benefit of also explaining boreotemperate patterns in 15N-depletion of ECM-associating host plants (Craine et al. 2009) and has been verified along successional chronosequences (Hobbie et al. 2005) and in the laboratory (Kohzu et al. 2000). It remains possible, however, that many sporocarps are further 15N enriched due to additional reasons. For instance, the preferential use of 15N-enriched N sources (e.g. protein and chitin) as well as internal processing and loss of isotopically light N compounds also have been posited to contribute to patterns of 15N enrichment in sporocarps (Brearley et al. 2005, Dijkstra et al. 2008, Hobbie et al. 2008). Hyphal exploration types (Hobbie and Agerer 2009, Agerer et al. 2012) and depth of mycelial growth (Lindahl et al. 2007) are also likely to contribute to the 15N enrichment of sporocarps for similar reasons related to the d15N value of distinct N sources.

Although the type of hyphal exploration type is currently unknown for most fungi, including those reported here (see DEEMY, www.deemy.de), and the isotopic values of the forms of N used by ECM fungi are also generally unknown, we can speculate as to possible reasons for above average 15N enrichment based on the ecological associations of many Clavariaceae fungi with members of the Ericaceae or other plants as discussed below. It is commonly held that some taxa of fungi can form both ecto- and ericoid mycorrhizal morphologies (Bergero et al. 2000) and that these fungi are believed to exhibit the enzymatic capacity for the degradation of numerous recalcitrant compounds (Lilliskov et al. 2002, Read and Perez-Moreno 2002). It is intriguing to speculate that the above average 15N enrichment present in *Clavaria*, *Clavulinopsis* and *Ramariopsis* may betray a protein or organic N-based nutritional mode.

Our results are very similar to those of Seitzman et al. (2011) for the Hygrophoraceae in the irregular isotopic ratios that are assigned in our analysis suggest strong biotrophy among non-lignicolous *Clavaria*ceae. It is interesting that both Hygrophoraceae and Clavariaceae are commonly encountered in similar habitats (grasslands in Europe and forests in North America) and quite

often close to each other. The Clavariaceae may be involved in a previously unknown nutritional status as suggested by Griffith et al. (2002) and Seitzman et al. (2011) for the Hygrophoraceae and Tedersoo et al. (2010) for both.

Analysis of GenBank environment sequences

Performing a meta analysis of published studies pertaining to the trophic strategies of various genera, Rinaldi et al. (2008) considered *Clavaria* (among other genera in the Clavariaceae) as saprotrophic. This study, however, neglected to report the ericoid associations of Seviour et al. (1973) and Englander and Hull (1980). Only two references under ‘‘root tip molecular’’ are cited (Burke et al. 2005, 2006). The GenBank reference sequence to which the root-tip samples (AY456373) were compared is not *Clavaria* sp. but instead *Clavulina* sp. based on BLAST similarity.

Of particular interest are environmental sequences EU691875 and EU692436 (*Picea glauca* rhizosphere samples), the former identified by us a *Ramariopsis*, the latter nearly identical to a *Clavaria flavipes* Pers.: Fr. sequence. Also, environmental sequence FM997944 (*Vaccinium uliginosum* hair root sample) is almost identical to *Clavaria argillacea*, the same species implicated in a mutualistic symbiosis with Ericaceous hosts (Englander and Hull 1980). These environmental data, although sparse, in combination with biotropic stable isotope signatures, suggest a biotrophic nutritional mode for non-lignicolous *Clavaria*ceae.

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Appendix

Table 4. Taxon sampling, geographic location, specimen-voucher information, sequence source, GenBank accession numbers, and notes from the Clavariaceae and Trechisporales nLSU-rRNA datasets.

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Anomoporia bombycina	USA, Colorado	CFMR:L-6240	Binder et al. 2010	GU187564	
Anomoporia kamtschatica	Sweden	Edman K426 (GB)	Larsson unpublished	DQ144615	
Camarophyllopsis atropuncta	United Kingdom, Wales	GG731 (TENN)	Matheny et al. 2007	EF535270	
Camarophyllopsis aff. *foetens*	USA, North Carolina, Haywood County, Big Creek	ECV4175 (TENN)	This Study	HQ877678	
Camarophyllopsis hymenocephala	USA, North Carolina	DJL95-081505	Matheny et al. 2006	DQ457679	
Camarophyllopsis hymenocephala	USA, North Carolina	DJL98-081505	Matheny et al. 2007	EF516628	
Camarophyllopsis schulzeri	United Kingdom, Wales	GG091005 (TENN)	Matheny et al. 2007	EF537888	
Camarophyllopsis schulzeri	Finland	Jacobsson 3453 (H)	Saar et al. unpublished	AM946415	
Camarophyllopsis soil clone	USA, Michigan	Man7_litter_E09	Edwards & Zak 2012	GU328638	O Horizon
Camarophyllopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	142a_04 KBS-LTER	Lynch & Thorn 2006	DQ341951	Agricultural soil
Camarophyllopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	150a_07 KBS-LTER	Lynch & Thorn 2006	DQ341972	Agricultural soil
Camarophyllopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	142a_01 KBS-LTER	Lynch & Thorn 2006	DQ341950	Agricultural soil
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A12YC19RM1	Zinger et al. 2009	FJ566279	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YN03RM1	Zinger et al. 2009	FJ565834	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A8YM09RM1	Zinger et al. 2009	FJ567914	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A1YN06RM1	Zinger et al. 2009	FJ566864	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YP06RM1	Zinger et al. 2009	FJ565854	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A12YK07RM1	Zinger et al. 2009	FJ566444	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A12YK07RM1	Zinger et al. 2009	FJ566394	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YE10RM1	Zinger et al. 2009	FJ565744	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YB23RM1	Zinger et al. 2009	FJ565714	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YD20RM1	Zinger et al. 2009	FJ565734	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A12YG17RM1	Zinger et al. 2009	FJ566369	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YP18RM1	Zinger et al. 2009	FJ565858	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A8YI18RM1	Zinger et al. 2009	FJ567831	Alpine tundra

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A1YO19RM1	Zinger et al. 2009	FJ566901	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YK03RM1	Zinger et al. 2009	FJ565799	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YF05RM1	Zinger et al. 2009	FJ565753	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YH09RM1	Zinger et al. 2009	FJ565777	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YE16RM1	Zinger et al. 2009	FJ565747	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A12YJ13RM1	Zinger et al. 2009	FJ566427	Alpine tundra
Camarophyllopsis soil clone group 2	France, Savoie, Massif du Grand Galibier	A10YK14RM1	Zinger et al. 2009	FJ565805	Alpine tundra
Clavaria alboglobospora	New Zealand, Northland, Waipoua Forest Reserve	TENN042295 (TENN)	This study	HQ877682	HOLOTYPE
Clavaria argillacea	Sweden	ELj98 (GB)	Larsson et al. 2004	AY463395	
Clavaria argillacea	Greenland, Qeqqata, Sisimiut	TFB10720 (TENN)	This study	HQ877683	
Clavaria citrinorubra	Australia	TENN040464 (TENN)	This study	HQ877686	HOLOTYPE
Clavaria cf. *falcata*	United Kingdom, Wales	GGAB05-32 (TENN)	Matheny et al. 2007	EF535278	Previously labeled *Clavaria fragilis*, labeled *Clavaria acuta*
Clavaria cf. *falcata*	USA, Washington, Mason County	JFA10440 (WTU)	This Study	HQ877680	
Clavaria cf. *falcata*	Sweden, Småland, Hylte, Femsjö	MTS4577 (WTU)	This Study	HQ877679	
Clavaria cf. *falcata*	New Zealand, Northland, Waipoua Forest Reserve	RHP55840 (TENN)	This Study	HQ877681	
Clavaria flavipes	United Kingdom, Wales	GG131104 (TENN)	Matheny et al. 2007	EF535267	Previously labeled *Clavaria straminea*
Clavaria flavipes	Canada, British Columbia, North Vancouver, Capilano Fish Hatchery	NH1 (UBC)	Haddad et al. unpublished	AY228353	Labeled *Clavaria acuta*; specimen examined and found to be *Clavaria flavipes*
Clavaria cf. *fragilis*	Minnesota, Nerstrand Big Woods State Park	DJM1262 (MIN)	Dentinger & McLaughlin 2006	DQ284907	Labeled *Clavaria vermicularis*
Clavaria cf. *fragilis*	USA, Tennessee, Cocke Co., Maddron Bald Trail	ADW0128 (TENN)	This study	HQ877687	
Clavaria cf. *fragilis*	USA, Washington, King Co., Seward Park	SAT98-349-01 (WTU)	This study	HQ877688	
Clavaria cf. *fragilis*	USA, Tennessee, Blount Co., Tremont	JMB081710003 (TENN)	This study	HQ877689	
Clavaria fumosa	United Kingdom, Wales	GG151003 (TENN)	Matheny et al. 2007	EF535268	
Clavaria cf. *fumosa*	USA, Tennessee, Sevier Co., Greenbrier	JMB100610005 (TENN)	This study	HQ877690	
Clavaria fuscata	USA, Tennessee, Sevier Co., Rainbow falls trail	JMB0818201001 (TENN)	This study	HQ877691	
Clavaria inaequalis	USA, Massachusetts	MB04-016 (TENN)	Matheny et al. 2007	AY745693	Previously labeled *Clavulinopsis laeticolor*
Clavaria pullei	Sweden	KGN98 (GB)	Larsson et al. 2004	AY586646	Previously labeled *Clavaria fumosa*

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria redoleoalii	New Zealand, Northland, Waipoua Forest Reserve	DJM1079 (MIN)	Dentinger & McLaughlin 2006	DQ284906	
Clavaria rosea	USA, Michigan, Pellston Co.	STZ9958 (WTU)	This study	HQ877694	
Clavaria cf. *rubicundula*	USA, Tennessee, Cocke Co., Low Gap Trail	SAT09-217-18 (TENN)	This study	HQ877695	
Clavaria cf. *rubicundula*	USA, Tennessee, Blount Co., Jakes Creek Trail	MR00170	This study	HQ877696	
Clavaria cf. *rubicundula*	New Zealand, Northland, Waipoua Forest Reserve	TENN043695	This study	HQ877697	
Clavaria stegasauroides	Australia, Tasmania, St. Columba Falls	PBM3373 (TENN)	This study	HQ877698	
Clavaria subacuta	Japan, Tochigi, Nikko, Lake Chuzenjiko	RHP2322 (TENN)	This study	HQ877699	
Clavaria zollingeri	USA, Tennessee, Blount Co., Jakes Creek trail	JMB08040912 (TENN)	This study	HQ877700	
Clavaria zollingeri	USA, Tennessee, Sevier Co., Cherokee Orchard	RHP9751 (TENN)	Matheny et al. 2007	AY639882	
Clavaria sp.	Russia, Primorsky	TFB11835 (TENN)	This Study	HQ877692	
Clavaria sp.	USA, Tennessee, Sevier Co., Rainbow Falls trailhead	JMB10061001 (TENN)	This study	HQ877684	
Clavaria sp.	Brazil, Parana	ADM1311 (TENN)	This study	HQ877685	
Clavaria sp. soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	080a_03 KBS-LTER	Lynch & Thorn 2006	DQ341797	Agricultural soil
Clavaria cf. *falcata* soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	141a_03 KBS-LTER	Lynch & Thorn 2006	DQ341946	Agricultural soil
Clavaria argillacea soil clone group	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	E12_OTU33	Taylor et al. 2007	EF433981	
Clavaria argillacea soil clone group	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TH10_OTU33	Taylor et al. 2007	EF434098	
Clavaria argillacea soil clone group	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag102_2119	Taylor et al. 2008	EU292494	
Clavaria argillacea soil clone group	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag126_4365	Taylor et al. 2008	EU292666	
Clavaria argillacea clone from *Vaccinium uliginosum* hair root	Sweden, Norbotten	OTU20	Kjoller et al. 2010	FM997944	Same as *Clavaria argillacea*
Clavaria fuscata soil clone	Canada, Ontario, York, Koffler Scientific Reserve	Ss2c12	Porter et al. 2008	EU522902	B-horizon from hemlock dominated forest
Clavaria flavipes soil clone	France, Savoie, Massif du Grand Galibier	A8YO02RM1	Zinger et al. 2009	FJ567953	Alpine tundra
Clavaria flavipes soil clone	France, Savoie, Massif du Grand Galibier	A1YF01RM1	Zinger et al. 2009	FJ566676	Alpine tundra
Clavaria flavipes soil clone	France, Savoie, Massif du Grand Galibier	A10YB13RM1	Zinger et al. 2009	FJ565706	Alpine tundra
Clavaria flavipes clone from *Picea glauca* rhizosphere		MWGM3T8_4F	Lamarche et al. 2011	EU692436	Same as *Clavaria straminea*
Clavaria soil clone	USA, Michigan	Man7_soil_D10	Edwards & Zak 2012	GU328628	

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A7YA17RM1	Zinger et al. 2009	FJ567301	Alpine tundra
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A9YM19RM1	Zinger et al. 2009	FJ568269	Alpine tundra
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A9YB23RM1	Zinger et al. 2009	FJ568036	Alpine tundra
Clavaria soil clone	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_AugA04	Hassett & Zak unpublished	GU174274	A Horizon
Clavaria soil clone	USA, Michigan, Manistee National Forest	OC_A_MayF08	Hassett & Zak unpublished	GU174361	A Horizon
Clavaria soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	080a_06 KBS-LTER	Lynch & Thorn 2006	DQ341800	Agricultural soil
Clavaria soil clone	USA, Michigan	Man6_soil_F09	Edwards & Zak 2012	GU328617	
Clavaria soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	157a_09 KBS-LTER	Lynch & Thorn 2006	DQ341993	Agricultural soil
Clavaria soil clone	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	H17_OTU43	Taylor et al. 2007	EF434089	O-horizon Soil
Clavaria soil clone	USA, Michigan	Man22_soil_F01	Edwards & Zak 2012	GU328506	
Clavaria soil clone	USA, Michigan	Man56_soil_E03	Edwards & Zak 2012	GU328580	
Clavaria soil clone	USA, Michigan	Man7_soil_E10	Edwards & Zak 2012	GU328631	
Clavaria soil clone	USA, Michigan	Man3_soil_F07	Edwards & Zak 2012	GU328545	
Clavaria soil clone	USA, Michigan	Man41_soil_F09	Edwards & Zak 2012	GU328564	
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A7YH19RM1	Zinger et al. 2009	FJ567454	Alpine tundra
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A11YM17RM1	Zinger et al. 2009	FJ566148	Alpine tundra
Clavaria soil clone	France, Savoie, Massif du Grand Galibier	A8YE09RM1	Zinger et al. 2009	FJ567731	Alpine tundra
Clavaria soil clone	Canada, Ontario, York, Koffler Scientific Reserve	Os3c13	Porter et al. 2008	EU522881	B-horizon from Hemlock dominated forest
Clavaria soil clone	Canada, Ontario, York, Koffler Scientific Reserve	4C71	Porter et al. 2008	EU522869	From Hemlock dominated forest
Clavaria soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	160a_12 KBS-LTER	Lynch & Thorn 2006	DQ342010	Agricultural soil
Clavaria soil clone	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TF5_OTU43	Taylor et al. 2007	EF434089	O-horizon Soil
Clavaria soil clone	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_698_SCHIRP10	Berbee & Dee unpublished	GQ159940	Salal, Cedar, Hemlock research forest
Clavaria soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	152a_12 KBS-LTER	Lynch & Thorn 2006	DQ341977	Agricultural soil
Clavaria soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	157a_01 KBS-LTER	Lynch & Thorn 2006	DQ341990	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone group 2	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	090a_09 KBS-LTER	Lynch & Thorn 2006	DQ341990	Agricultural soil
Clavaria soil clone group 2	France, Savoie, Massif du Grand Galibier	A1YE06RM1	Zinger et al. 2009	FJ566659	Alpine tundra
Clavaria soil clone group 2	France, Savoie, Massif du Grand Galibier	A1YB20RM1	Zinger et al. 2009	FJ566609	Alpine tundra
Clavaria soil clone group 3	France, Savoie, Massif du Grand Galibier	A9YM09RM1	Zinger et al. 2009	FJ568259	Alpine tundra
Clavaria soil clone group 3	France, Savoie, Massif du Grand Galibier	A9YJ22RM1	Zinger et al. 2009	FJ568205	Alpine tundra
Clavaria soil clone group 3	France, Savoie, Massif du Grand Galibier	A7YB05RM1	Zinger et al. 2009	FJ567313	Alpine tundra
Clavaria soil clone group 3	France, Savoie, Massif du Grand Galibier	A7YP19RM1	Zinger et al. 2009	FJ567630	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YA19RM1	Zinger et al. 2009	FJ566947	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YC23RM1	Zinger et al. 2009	FJ566992	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YD05RM1	Zinger et al. 2009	FJ566998	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YA02RM1	Zinger et al. 2009	FJ566930	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YB19RM1	Zinger et al. 2009	FJ566966	Alpine tundra
Clavaria soil clone group 4	France, Savoie, Massif du Grand Galibier	A2YA22RM1	Zinger et al. 2009	FJ566950	Alpine tundra
Clavaria soil clone group 5	France, Savoie, Massif du Grand Galibier	A11YL01RM1	Zinger et al. 2009	FJ566110	Alpine tundra
Clavaria soil clone group 5	France, Savoie, Massif du Grand Galibier	A11YK04RM1	Zinger et al. 2009	FJ566090	Alpine tundra
Clavaria soil clone group 6	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	143a_03 KBS-LTER	Lynch & Thorn 2006	DQ341956	Agricultural soil
Clavaria soil clone group 6	USA, Colorado, Boulder Co., Niwot Ridge LTER	FunCon5_10F	Nemergut et al. 2008	EU861814	Alpine tundra dry meadow surface soil
Clavaria soil clone group 6	USA, Colorado, Boulder Co., Niwot Ridge LTER	FunCON4_03B	Nemergut et al. 2008	EU861758	Alpine tundra dry meadow surface soil
Clavaria soil clone group 6	USA, Colorado, Boulder Co., Niwot Ridge LTER	FunCon5_04E	Nemergut et al. 2008	EU861799	Alpine tundra dry meadow surface soil
Clavaria soil lone group 7	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	149a_06 KBS-LTER	Lynch & Thorn 2006	DQ341963	Agricultural soil
Clavaria soil lone group 7	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	132a_05 KBS-LTER	Lynch & Thorn 2006	DQ341923	Agricultural soil
Clavaria soil lone group 7	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	130a_05 KBS-LTER	Lynch & Thorn 2006	DQ341921	Agricultural soil
Clavaria soil lone group 7	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	054a_06 KBS-LTER	Lynch & Thorn 2006	DQ341702	Agricultural soil
Clavaria soil clone group 8	France, Savoie, Massif du Grand Galibier	A10YK12RM1	Zinger et al. 2009	FJ565804	Alpine tundra
Clavaria soil clone group 8	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	157a_08 KBS-LTER	Lynch & Thorn 2006	DQ341992	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone group 8	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	158a_02 KBS-LTER	Lynch & Thorn 2006	DQ341996	Agricultural soil
Clavaria soil clone group 8	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_MayH02	Hassett & Zak unpublished	GU174395	A Horizon
Clavaria soil clone group 9	USA, Michigan, Manistee National Forest	OC_A_AugE11	Hassett & Zak unpublished	GU174373	A Horizon
Clavaria soil clone group 9	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_MayD03	Hassett & Zak unpublished	GU174394	A Horizon
Clavaria soil clone group 10	USA, Michigan	Man56_soil_B04	Edwards & Zak 2012	GU328577	
Clavaria soil clone group 10	USA, Michigan	Man56_litter_A06	Edwards & Zak 2012	GU328581	O Horizon
Clavaria soil clone group 11	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_MayC01	Hassett & Zak unpublished	GU174390	A Horizon
Clavaria soil clone group 11	USA, Michigan, Manistee National Forest	OC_A_MayA07	Hassett & Zak unpublished	GU174429	A Horizon
Clavaria soil clone group 12	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_MayD05	Hassett & Zak unpublished	GU174319	A Horizon
Clavaria soil clone group 12	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_AugF04	Hassett & Zak unpublished	GU174340	A Horizon
Clavaria soil clone group 12	USA, Tennessee, Roane Co., Oak Ridge National Laboratory	Fung.wet.ACATFAC07	Castro et al. 2010	GU375891	Oil-field Soil
Clavaria soil clone group 12	USA, Tennessee, Roane Co., Oak Ridge National Laboratory	Fung.wet.ECETFDF06	Castro et al. 2010	GU376129	Oil-field Soil
Clavaria soil clone group 12	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	151a_01 KBS-LTER	Lynch & Thorn 2006	DQ341973	Agricultural soil
Clavaria soil clone group 12	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	151a_02 KBS-LTER	Lynch & Thorn 2006	DQ341974	Agricultural soil
Clavaria soil clone group 12	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	158a_05 KBS-LTER	Lynch & Thorn 2006	DQ341998	Agricultural soil
Clavaria soil clone group 13	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	141a_14 KBS-LTER	Lynch & Thorn 2006	DQ341949	Agricultural soil
Clavaria soil clone group 13	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	141a_07 KBS-LTER	Lynch & Thorn 2006	DQ341947	Agricultural soil
Clavaria soil clone group 14	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	109a_06 KBS-LTER	Lynch & Thorn 2006	DQ341855	Agricultural soil
Clavaria soil clone group 14	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	109a_15 KBS-LTER	Lynch & Thorn 2006	DQ341858	Agricultural soil
Clavaria soil clone group 14	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	046a_12 KBS-LTER	Lynch & Thorn 2006	DQ341679	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone group 14	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	067a_07 KBS-LTER	Lynch & Thorn 2006	DQ341751	Agricultural soil
Clavaria soil clone group 14	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	076a_12 KBS-LTER	Lynch & Thorn 2006	DQ341791	Agricultural soil
Clavaria soil clone group 14	USA, Michigan, Baraga Co., Baraga State Park	Alb_A_AugC08	Hassett & Zak unpublished	GU174286	A Horizon
Clavaria soil clone group 15	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	053a_01 KBS-LTER	Lynch & Thorn 2006	DQ341692	Agricultural soil
Clavaria soil clone group 15	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	046a_01 KBS-LTER	Lynch & Thorn 2006	DQ341676	Agricultural soil
Clavaria soil clone group 15	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	150a_01 KBS-LTER	Lynch & Thorn 2006	DQ341970	Agricultural soil
Clavaria soil clone group 15	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	150a_03 KBS-LTER	Lynch & Thorn 2006	DQ341971	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	046a_06 KBS-LTER	Lynch & Thorn 2006	DQ341678	Agricultural soil
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YD10RM1	Zinger et al. 2009	FJ565731	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YE03RM1	Zinger et al. 2009	FJ565739	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YE14RM1	Zinger et al. 2009	FJ566321	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YC18RM1	Zinger et al. 2009	FJ566278	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YF08RM1	Zinger et al. 2009	FJ566339	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YH11RM1	Zinger et al. 2009	FJ566387	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YH02RM1	Zinger et al. 2009	FJ565771	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YK18RM1	Zinger et al. 2009	FJ565807	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YO07RM1	Zinger et al. 2009	FJ565846	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YF06RM1	Zinger et al. 2009	FJ565754	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YH11RM1	Zinger et al. 2009	FJ565779	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YF13RM1	Zinger et al. 2009	FJ566343	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YG06RM1	Zinger et al. 2009	FJ565765	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YI08RM1	Zinger et al. 2009	FJ566405	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A12YI08RM1	Zinger et al. 2009	FJ565719	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YG09RM1	Zinger et al. 2009	FJ565767	Alpine tundra
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	065a_1.02 KBS-LTER	Lynch & Thorn 2006	DQ341739	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	074a_02 KBS-LTER	Lynch & Thorn 2006	DQ341780	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	066a_05 KBS-LTER	Lynch & Thorn 2006	DQ341743	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	067a_16 KBS-LTER	Lynch & Thorn 2006	DQ341756	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	074a_08 KBS-LTER	Lynch & Thorn 2006	DQ341783	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	160a_01 KBS-LTER	Lynch & Thorn 2006	DQ342007	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	160a_02 KBS-LTER	Lynch & Thorn 2006	DQ342008	Agricultural soil
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A10YK04RM1	Zinger et al. 2009	FJ565800	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YE14RM1	Zinger et al. 2009	FJ566666	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A7YN07RM1	Zinger et al. 2009	FJ567582	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A8YE18RM1	Zinger et al. 2009	FJ567740	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YA11RM1	Zinger et al. 2009	FJ566579	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YC04RM1	Zinger et al. 2009	FJ566613	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YO12RM1	Zinger et al. 2009	FJ566894	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YM04RM1	Zinger et al. 2009	FJ566838	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YJ11RM1	Zinger et al. 2009	FJ566779	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A8YH04RM1	Zinger et al. 2009	FJ567794	Alpine tundra
Clavaria soil clone group 16	France, Savoie, Massif du Grand Galibier	A1YG19RM1	Zinger et al. 2009	FJ566718	Alpine tundra
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	160a_05 KBS-LTER	Lynch & Thorn 2006	DQ342009	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	149a_13 KBS-LTER	Lynch & Thorn 2006	DQ341968	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	066a_10 KBS-LTER	Lynch & Thorn 2006	DQ341747	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	149a_10 KBS-LTER	Lynch & Thorn 2006	DQ341967	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	055a_01 KBS-LTER	Lynch & Thorn 2006	DQ341705	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	066a_07 KBS-LTER	Lynch & Thorn 2006	DQ341744	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	51a_12 KBS-LTER	Lynch & Thorn 2006	DQ341976	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	158a_04 KBS-LTER	Lynch & Thorn 2006	DQ341997	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	109a_14 KBS-LTER	Lynch & Thorn 2006	DQ341857	Agricultural soil
Clavaria soil clone group 16	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	158a_13 KBS-LTER	Lynch & Thorn 2006	DQ342001	Agricultural soil
Clavicorona taxophila		Strain 9186		AF115333	
Clavicorona taxophila	Idaho, Shoshone Co., Coeur D'Alene National Forest	RHP5608 (TENN)	This study	HQ877701	NEOTYPE
Clavulinopsis amoena	Australia, Tasmania, the Blue Tier, Goblin Track	PBM3381 (TENN)	This study	HQ877702	
Clavulinopsis antillarum	Australia, Tasmania, Mount Field National Park	PBM3446 (TENN)	This study	HQ877710	
Clavulinopsis aff. *aurantiocinnabarina*	USA, Tennessee, Knox Co., IJAMS Nature Center	JMB08240901 (TENN)	This study	HQ877703	
Clavulinopsis aff. *aurantiocinnabarina*	USA, Tennessee, Blount Co., Tremont	JMB08171004 (TENN)	This study	HQ877704	
Clavulinopsis aff. *aurantiocinnabarina*	USA, Tennessee, Blount Co., Tremont	JMB08171006 (TENN)	This study	HQ877705	
Clavulinopsis cf. *aurantiocinnabarina*	USA, West Virginia, Preston Co., Coopers Rock State Forest	PBM3010 (TENN)	This study	HQ877706	
Clavulinopsis aurantio-olivacea ined.	New Zealand, Northland, Omahuta Forest	RHP55850 (TENN)	This study	HQ877711	HOLOTYPE, in *Clavulinopsis* clade
Clavulinopsis corallinorosacea	Australia, Tasmania, the Blue Tier, Goblin Track	PBM3380 (TENN)	This study	HQ877710	
Clavulinopsis corniculata	USA, Tennessee, Cocke Co., Low Gap Trail	SAT0921720 (TENN)	This study	HQ877713	
Clavulinopsis fusiformis	USA, Massachusetts, Redemption Rock	PBM2804 (TENN)	Matheny et al. 2007	EF535273	
Clavulinopsis fusiformis	USA, Tennessee, Blount Co., Jakes Creek Trail	MGW672 (TENN)	This study	HQ877717	
Clavulinopsis gracillima	USA, Tennessee, Blount Co., Jakes Creek Trail	JMB10071002 (TENN)	This study	HQ877708	
Clavulinopsis gracillima soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	053a_10 KBS-LTER	Lynch & Thorn 2006	DQ341696	Agricultural soil
Clavulinopsis gracillima soil clone	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_908_SCHIRP8	Berbee & Dee unpublished	GQ159936	Salal, Cedar, Hemlock research forest
Clavulinopsis helvola	Sweden	RD990908 (GB)	Larsson et al. 2004	AY586647	
Clavulinopsis helvola	Sweden	EL 111/04 (GB)	Larsson 2007	EU118617	
Clavulinopsis laeticolor	Finland	EL8/00 (GB)	Larsson 2007	EU118618	
Clavulinopsis laeticolor soil clone	Canada, Ontario, York, Koffler Scientific Reserve	Os3c68	Porter et al. 2008	EU522887	B-horizon from hemlock dominated forest
Clavulinopsis novo-zealandica ined.	New Zealand, Wellington, Upper Hutt	TENN043575 (TENN)	This study	HQ877693	HOLOTYPE

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavulinopsis sulcata Over.	New Zealand, Bay of Plenty, Aongatete Lodge	PDD78241 (PDD)	Dentinger & McLaughlin 2006	DQ284904	
Clavulinopsis sulcata Over.	Australia, Tasmania, the Blue Tier, Goblin Track	PBM3379 (TENN)	This study	HQ877709	
Clavulinopsis soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	156a_09 KBS-LTER	Lynch & Thorn 2006	DQ341988	Agricultural soil
Clavulinopsis soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	063a_06 KBS-LTER	Lynch & Thorn 2006	DQ341736	Agricultural soil
Clavulinopsis soil clone	France, Savoie, Massif du Grand Galibier	A2YL08RM1	Zinger et al. 2009	FJ567184	Alpine tundra
Clavulinopsis soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	156a_09 KBS-LTER	Lynch & Thorn 2006	DQ341728	Agricultural soil
Clavulinopsis soil clone group 1	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_692_SCHIRP9	Berbee & Dee unpublished	GQ159938	Salal, Cedar, Hemlock research forest
Clavulinopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	066a_08 KBS-LTER	Lynch & Thorn 2006	DQ341745	Agricultural soil
Clavulinopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	067a_02 KBS-LTER	Lynch & Thorn 2006	DQ341748	Agricultural soil
Clavulinopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	068a_04 KBS-LTER	Lynch & Thorn 2006	DQ341757	Agricultural soil
Clavulinopsis soil clone group 1	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	073a_07 KBS-LTER	Lynch & Thorn 2006	DQ341778	Agricultural soil
Clavulinopsis soil clone group 2	Japan, Ibaraki, Ibaraki University College of Agriculture Field Science center	IU-FSC Fun73_FuD121	Nishizawa et al. 2010	AB520598	Non-tilled, cover cropped upland Rice field
Clavulinopsis soil clone group 2	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	143a_04 KBS-LTER	Lynch & Thorn 2006	DQ341957	Agricultural soil
Clavulinopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	155a_01 KBS-LTER	Lynch & Thorn 2006	DQ341983	Agricultural soil
Clavulinopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	155a_02 KBS-LTER	Lynch & Thorn 2006	DQ341984	Agricultural soil
Clavulinopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	155a_11 KBS-LTER	Lynch & Thorn 2006	DQ341985	Agricultural soil
Clavulinopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	155a_13 KBS-LTER	Lynch & Thorn 2006	DQ341986	Agricultural soil
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YM08RM1	Zinger et al. 2009	FJ567913	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YF06RM1	Zinger et al. 2009	FJ566681	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YI07RM1	Zinger et al. 2009	FJ566753	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YF19RM1	Zinger et al. 2009	FJ566694	Alpine tundra

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YK12RM1	Zinger et al. 2009	FJ567873	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YJ03RM1	Zinger et al. 2009	FJ567840	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YA09RM1	Zinger et al. 2009	FJ567641	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YG11RM1	Zinger et al. 2009	FJ567778	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YL19RM1	Zinger et al. 2009	FJ567901	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YO11RM1	Zinger et al. 2009	FJ566893	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YM12RM1	Zinger et al. 2009	FJ566846	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YH15RM1	Zinger et al. 2009	FJ566737	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YK02RM1	Zinger et al. 2009	FJ566792	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YF24RM1	Zinger et al. 2009	FJ566699	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YI22RM1	Zinger et al. 2009	FJ566767	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YK23RM1	Zinger et al. 2009	FJ566811	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YD23RM1	Zinger et al. 2009	FJ567721	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YL11RM1	Zinger et al. 2009	FJ567894	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YF08RM1	Zinger et al. 2009	FJ567754	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YG21RM1	Zinger et al. 2009	FJ567787	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YL09RM1	Zinger et al. 2009	FJ567893	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YI04RM1	Zinger et al. 2009	FJ567818	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YO13RM1	Zinger et al. 2009	FJ567962	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YA01RM1	Zinger et al. 2009	FJ567635	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A1YE09RM1	Zinger et al. 2009	FJ566662	Alpine tundra
Clavulinopsis soil clone group 4	France, Savoie, Massif du Grand Galibier	A8YE03RM1	Zinger et al. 2009	FJ567725	Alpine tundra
Hyphodontaceae soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	149a_07 KBS-LTER	Lynch & Thorn 2006	DQ341964	Agricultural soil
Hyphodontaceae soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	149a_14 KBS-LTER	Lynch & Thorn 2006	DQ341969	Agricultural soil
Hyphodontiella multiseptata	Sweden	Ryberg 021022 (GB)	Larsson 2007	EU118634	
Mucronella bresadolae	Canada, Brirish Columbia, Vancouver, Capilano River Regional Park	F15204 (UBC)	Berbee et al. unpublished	DQ384591	
Mucronella calva		GEL4458 (TUB)	Langer unpublished	AJ406588	
Mucronella calva	Norway	JS16142 (GB)	Larsson et al. 2004	AY586689	

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Mucronella aff. *calva*	USA, Puerto Rico	KHL10317 (GB)	Larsson et al. 2004	AY586690	
Mucronella fusiformis	USA, Oregon, Lincoln Co, Cape Perpetua	DJM1309 (MIN)	Dentinger & McLaughlin 2006	DQ284905	
Mucronella sp.	South Korea	KUC8367 (KUS)	Kim et al. 2009	FJ471546	
Mucronella sp.	South Korea	KUC8381 (KUS)	Kim et al. 2009	FJ471564	
Mucronella pendula	Australia, Tasmania, Mount Field National Park	PBM3437 (TENN)	This study	HQ829921	
Phlebiella vaga	Denmark	NH10396 (GB)	Larsson et al. 2004	AY586696	
Phlebiella vaga	Sweden	KHL 11065 (GB)	Larsson 2007	EU118661	
Plicaturopsis crispa		FP-101310-SP	Binder et al. 2005	AY293203	
Podoserpula pusio	Australia, Australia Capital Territory	HLepp 329	Matheny et al. unpublished	EF535271	
Porpomyces mucidus		KHL 11062 (GB)	Larsson unpublished	AF347091	
Porpomyces mucidus		KHL 8620 (GB)	Larsson unpublished	AF347092	
Porpomyces mucidus		KHL 8471 (GB)	Larsson unpublished	AF347093	
Porpomyces mucidus	Czech Republic	BRNM 710171	Tomsovsky et al. 2010	FJ496696	
Ramariopsis biformis	USA, Tennessee, Sevier Co., Greenbrier	JMB10061001 (TENN)	This study	HQ877712	
Ramariopsis biformis soil clone	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_696_SCHIRP6	Berbee & Dee unpublished	GQ159933	Salal, Cedar, Hemlock research forest
Ramariopsis cremicolor	New Zealand, Bay of Plenty	RHP55875 (TENN)	This study	HQ877714	HOLOTYPE
Ramariopsis cremicolor	New Zealand, Wellington, Kaitoke Regional Park	DJM1049 (MIN)	Dentinger & McLaughlin 2006	DQ284903	Labeled *Ramariopsis* sp.
Ramariopsis crocea f. *conspicua*	USA, Idaho, Bonner Co., Upper Priest River	RHP3595 (TENN)	This study	HQ877716	HOLOTYPE
Ramariopsis crocea	USA, Tennessee, Blount Co., Jakes Creek Trail	JMB10071001 (TENN)	This study	HQ877715	
Ramariopsis crocea soil clone	France, Savoie, Massif du Grand Galibier	A11YH08RM1	Zinger et al. 2009	FJ566027	Alpine tundra
Ramariopsis junquillea	New Zealand, Bay of Plenty, Te Urewera National Park	RHP55786 (TENN)	This study	HQ877718	HOLOTYPE
Ramariopsis kunzei	United Kingdom, Wales	GG141104 (TENN)	Matheny et al. 2007	EF561638	
Ramariopsis aff. *kunzei*	USA, Minnesota, Rice Co., Nerstrand-Big Woods State Park	BD346 (MIN)	Dentinger & McLaughlin 2006	DQ284902	
Ramariopsis aff. *kunzei*	USA, Tennessee, Blount Co., Jakes Creek Trail	MR00183 (TENN)	This study	HQ877720	
Ramariopsis aff. *kunzei*	USA, Tennessee, Blount Co., Jakes Creek Trail	JMB10071005 (TENN)	This study	HQ877721	
Ramariopsis aff. *kunzei* soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	047a_06 KBS-LTER	Lynch & Thorn 2006	DQ341683	Agricultural soil
Ramariopsis pseudosubtilis	USA, Tennessee, Blount Co., Sugar Cove	RHP2344 (TENN)	This study	HQ877723	HOLOTYPE

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Ramariopsis tenuiramosa	United Kingdom, Wales	GG061104 (TENN)	Matheny et al. 2007	EF535269	
Ramariopsis sp.	USA, California, Del Norte, Co., Jedediah Smith Redwoods State Park	RHP55462 (TENN)	This study	HQ877722	
Ramariopsis clone group 8 from *Picea glauca* rhizosphere	Canada, Quebec	MWCt11T0_3E	Lamarche et al. 2011	EU691875	*Picea glauca* rhizosphere
Ramariopsis soil clone	France, Savoie, Massif du Grand Galibier	A9YB10RM1	Zinger et al. 2009	FJ568024	Alpine tundra
Ramariopsis soil clone	Japan, Ibaraki, Ibaraki University College of Agriculture Field Science center	IU0FSC Fun73_FuA089	Nishizawa et al. 2010	AB520596	Non-tilled, cover cropped upland Rice field
Ramariopsis soil clone	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	053a_04 KBS-LTER	Lynch & Thorn 2006	DQ341694	Agricultural soil
Ramariopsis soil clone	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_690_SCHIRP9	Berbee & Dee unpublished	GQ159937	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone	Japan, Ibaraki, Ibaraki University College of Agriculture Field Science center	IU-FSC Fun73_FuA088	Nishizawa et al. 2010	AB520595	Non-tilled, cover cropped upland Rice field
Ramariopsis soil clone	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_691_SCHIRP9	Berbee & Dee unpublished	GQ159939	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 1	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_0185	Taylor et al. 2008	EU292224	
Ramariopsis soil clone group 1	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_4213	Taylor et al. 2008	EU292320	
Ramariopsis soil clone group 1	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag126_0915	Taylor et al. 2008	EU292586	
Ramariopsis soil clone group 2	Japan, Ibaraki, Ibaraki University College of Agriculture Field Science Center	IU-FSC Fun73_FuB137	Nishizawa et al. 2010	AB520597	Non-tilled, cover cropped upland rice field
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TC4_OTU44	Taylor et al. 2007	EF434069	O-horizon Soil
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	L9_OTU44	Taylor et al. 2007	EF434030	O-horizon Soil
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag102_4594	Taylor et al. 2008	EU292560	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_0716	Taylor et al. 2008	EU292234	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TKN13_3300_J18	Geml et al. 2010	EU712188	As uncultered Russulaceae clone
Ramariopsis soil clone group 2	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_697_SCHIRP4	Berbee & Dee unpublished	GQ159930	Salal, Cedar, Hemlock research forest

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag126_0353	Taylor et al. 2008	EU292568	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag067_2518	Taylor et al. 2008	EU292385	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_1421	Taylor et al. 2008	EU292241	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag102_2576	Taylor et al. 2008	EU292508	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag102_0186	Taylor et al. 2008	EU292451	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag102_3225	Taylor et al. 2008	EU292526	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag067_3276	Taylor et al. 2008	EU292406	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_2805	Taylor et al. 2008	EU292273	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag064_2757	Taylor et al. 2008	EU292270	
Ramariopsis soil clone group 2	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	IH_Tag126_4196	Taylor et al. 2008	EU292660	
Ramariopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	062a_02 KBS-LTER	Lynch & Thorn 2006	DQ341729	Agricultural soil
Ramariopsis soil clone group 3	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	063a_03 KBS-LTER	Lynch & Thorn 2006	DQ341735	Agricultural soil
Ramariopsis soil clone group 4	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	L18_OTU45	Taylor et al. 2007	EF434027	O-horizon Soil
Ramariopsis soil clone group 4	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TP7_OTU45	Taylor et al. 2007	EF434153	O-horizon Soil
Ramariopsis soil clone group 5	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_695_SCHIRP7	Berbee & Dee unpublished	GQ159934	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 5	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_694_SCHIRP7	Berbee & Dee unpublished	GQ159935	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 6	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_700_SCHIRP5	Berbee & Dee unpublished	GQ159931	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 6	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_699_SCHIRP5	Berbee & Dee unpublished	GQ159932	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 7	USA, Alaska, Fairbanks North Star Borough, Bonanza Creek LTER	TJ20_OTU179	Taylor et al. 2007	EF434117	O-horizon Soil
Ramariopsis soil clone group 7	USA, Michigan, Kalamazoo Co., W.G. Kellogg Biological Station	066a_01 KBS-LTER	Lynch & Thorn 2006	DQ341741	Agricultural soil

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Ramariopsis soil clone group 8	USA, Wisconsin, Oneida Co., FACTS-II FACE site	Bas07166	Edwards & Zak 2011	HQ433218	Soil beneath Aspen
Ramariopsis soil clone group 8	Canada, British Columbia, Mount Waddington, Port McNeill	JDUBC_693_SCHIRP11	Berbee & Dee unpublished	GQ159941	Salal, Cedar, Hemlock research forest
Ramariopsis soil clone group 8	USA, Colorado, Boulder Co., Niwot Ridge LTER	FunCON5_12A	Nemergut et al. 2008	EU861817	Alpine tundra dry meadow surface soil
Scytinopogon angulisporus	USA, Tennessee, Sevier Co., Cherokee Orchard	TFB13611 (TENN)	This study	JQ684661	
Sistotremastrum niveocremeum	Sweden	EL 96-97 (GB)	Larsson et al. 2004	AF347094	
Sistotremastrum suecicum	Sweden	KHL 11849 (GB)	Larsson 2007	EU118667	
Sistotremastrum sp.		FO36293b	Langer unpublished	AJ406425	
Subulicystidium longisporum		GEL5217a	Langer unpublished	AJ406422	
Subulicystidium sp.	Jamaica	KHL10780 (GB)	Larsson et al. 2004	AY586714	
Trechispora alnicola		CBS577.83	Matheny et al. 2007	AY635768	
Trechispora araneosa		KHL 8570 (GB)	Larsson unpublished	AF347084	
Trechispora confinis	Sweden	KHL 11064 (GB)	Larsson unpublished	AF347081	
Trechispora confinis	Sweden	KHL11197 (GB)	Larsson et al. 2004	AY586719	
Trechispora farinacea		KHL 8451 (GB)	Larsson unpublished	AF347082	
Trechispora farinacea		KHL 8454 (GB)	Larsson unpublished	AF347083	
Trechispora farinacea	Sweden	KHL 8793 (GB)	Larsson 2004	AF347089	
Trechispora hymenocystis	Sweden	KHL 8795 (GB)	Larsson 2004	AF347090	
Trechispora incisa		EH 24/98 (GB)	Larsson unpublished	AF347085	
Trechispora kavinioides	Norway	KGN 981002 (GB)	Larsson unpublished	AF347086	
Trechispora nivea	Norway	G. Kristiansen s.n.	Larsson 2004	AY586720	
Trechispora regularis	Jamaica	KHL 10881 (GB)	Larsson unpublished	AF347087	
Trechispora subsphaerospora	Sweden	KHL 8511 (GB)	Larsson unpublished	AF347080	
Trechispora thelephora	Belize	UTC 252606	Albee-Scott & Kropp unpublished	HM104485	
Trechispora sp.	USA, Washington, King Co., Hazel Wolf Wetlands	PBM418	Matheny et al. 2007	AY647217	
Trechispora sp.		TMB 17a	Matsuura & Yashiro 2010	FJ232039	
Trechispora sp.		TMB 19a	Matsuura & Yashiro 2010	FJ232040	
Trechispora sp.		TMB 21.1	Matsuura & Yashiro 2010	FJ232041	

Table 4 Continued

Species	Geographic location	Specimen Voucher/Clone	Sequence source	GenBank Accession No.	Notes (habitat, taxonomic, other)
Trechispora sp.		TMB 22.9	Matsuura & Yashiro 2010	FJ232042	
Trechispora sp.		TMB 38b	Matsuura & Yashiro 2010	FJ232043	
Tubulicium vermiculare		GEL5015	Langer unpublished	AJ406424	
Tubulicium vermiferum	Norway	KHL8714 (GB)	Larsson et al 2004	AY463477	

Table 5. List of specimens used in a discriminant multivariate analysis using fungal $\delta^{15}N$ and $\delta^{13}C$ isotope values and collector-based categorizations of nutritional mode: biotrophic (BIO) vs. saprotrophic (SAP). Replicate samples are shaded gray.

No.	Specimen-voucher	Geographic location	Habitat	Species	δ15N (‰)	δ13C (‰)	Nutritional mode prediction	Prob.	δ15N analytical SE	δ13C analytical SE
1	PBM3238	Tasmania	on soil in dry sclerophyll forest	*Porpoloma* sp.	7.78	-23.25	BIO	94%		
2	PAM10102001	France	on soil unimproved grassland	*Camarophyllopsis atropuncta*	11.18	-25.64	BIO	100 %		
3	ADW0128	Tennessee	on soil in cove hardwood forest	*Clavaria fragilis*	13.16	-23.79	BIO	100 %		
4	JMB081810-01	Tennessee	on soil in cove hardwood forest	*Clavaria zollingeri*	12.73	-26.37	BIO	100 %		
5a	SAT10-283-03	Tennessee	on soil in cove hardwood forest	*Ramariopsis kunzei*	13.86	-24.89	BIO	100 %	0.045	0.662
5b	SAT10-283-03	Tennessee	on soil in cove hardwood forest	*R. kunzei*	13.8	-25.94	BIO			
5c	SAT10-283-03	Tennessee	on soil in cove hardwood forest	*R. kunzei*	13.71	-27.18	BIO			
6	SAT09-216-04	Tennessee	on soil in cove hardwood forest	*Ramariopsis fusiformis*	16.02	-26.32	BIO	100 %		
7	SAT09-217-20	Tennessee	on soil in cove hardwood forest	*Ramariopsis corniculata*	13.82	-25.98	BIO	100 %		
8	PBM3379	Tasmania	on soil in mixed *Nothofagus*, *Leptospermum* rainforest	*Clavulinopsis sulcata*	15.72	-29.8	BIO	100 %		

Table 5 Continued

No.	Specimen-voucher	Geographic location	Habitat	Species	δ15N (‰)	δ13C (‰)	Nutritional mode prediction	Prob.	δ15N analytical SE	δ13C analytical SE
9	JMB100810-01	Tennessee	on soil in Eastern Hemlock forest	*Clavaria* sp.	12.35	-23.14	BIO	100%		
10a	SAT10-173-02	Tennessee	on soil in cove hardwood forest	*Clavaria zollingeri*	12.32	-25.44	BIO	100%	0.022	0.704
10b	SAT10-173-02	Tennessee	on soil in cove hardwood forest	*C. zollingeri*	12.32	-26.09				
10c	SAT10-173-02	Tennessee	on soil in cove hardwood forest	*C. zollingeri*	12.39	-23.73				
11	BPL10	Tennessee	on soil in cove hardwood forest	*Clavaria fragilis*	15.24	-26.42	BIO	100%		
12	MGW672	Tennessee	on soil in cove hardwood forest	*Ramariopsis fusiformis*	20.54	-27.38	BIO	100%		
13	JMB100610-02	Tennessee	on soil in Eastern Hemlock forest	*Ramariopsis laeticolor*	11.45	-26.16	BIO	100%		
14	SAT09-209-04	Tennessee	on soil in cove hardwood forest	*Ramariopsis fusiformis*	14.3	-24.51	BIO	100%		
15	SAT09-214-17	North Carolina	on soil in cove hardwood forest	*Ramariopsis kunzei*	14.61	-24.19	BIO	100%		
16	ECV4038	Tennessee	on soil in cove hardwood forest	Leucopaxilleae “gray scaly”	13.1	-24.03	BIO	100%		
17	ECV4049	Tennessee	on soil in cove hardwood forest	Leucopaxilleae “mystery white”	9.08	-25.86	BIO	100%		
18	PBM3514	Tennessee	on ground under planted *Pinus strobus*, *Quercus phellos*	*Leucopaxillus laterarius*	12.01	-21.2	BIO	97%		
19	JFA SU	California	on soil in Northern California coastal forest	*Clavaria fragilis*	14.08	-23.34	BIO	100%		
20	PBM3010	West Virginia	on soil in hardwood forest	*Clavulinopsis aurantiocinnabarina*	16.82	-28.09	BIO	100%		
21	JFA10440	Washington	on soil in lowland conifer forest	*Clavaria acuta*	9.22	-22.57	BIO	96%		
22	SAT10-173-11	Tennessee	on soil in cove hardwood forest	*Clavaria zollingeri*	13.25	-25.67	BIO	100%		

Table 5 Continued

No.	Specimen-voucher	Geographic location	Habitat	Species	δ15N (‰)	δ13C (‰)	Nutritional mode prediction	Prob.	δ15N analytical SE	δ13C analytical SE
23	ECV4142	North Carolina	on soil in cove hardwood forest	Leucopaxilleae "mystery white"	7.33	-24.53	BIO	99%		
24	JMB100610-04	Tennessee	on soil in cove hardwood forest	*Ramariopsis kunzei*	13	-25.94	BIO	100%		
25	MGW676	Tennessee	on soil in Eastern Hemlock forest	Leucopaxillae, white, undet.	10.28	-25.7	BIO	100%		
26a	ECV4175	North Carolina	on soil in cove hardwood forest	*Camarophyllopsis foetens*	5.93	-23.77	BIO	89%	0.108	0.912
26b	ECV4175	North Carolina	on soil in cove hardwood forest	*Cm. foetens*	6.14	-25.59				
27	MGW832	Tennessee	on soil in cove hardwood forest	*Dennisiomyces* sp.	0.95	-24.52	Equivocal	50%		
28a	DJL-NC-15-05	North Carolina	on soil in cove hardwood forest	*Leucopaxillus tricolor*	10.47	-22.9	BIO	99%	0.07	0.429
28b	DJL-NC-15-05	North Carolina	on soil in cove hardwood forest	*L. tricolor*	10.33	-23.75	BIO			
28c	DJL-NC-15-05	North Carolina	on soil in cove hardwood forest	*L. tricolor*	10.23	-22.27	BIO			
29	PBM3060	Tennessee	on soil under planted *Pinus strobus*, *Quercus phellos*	*Leucopaxillus lateritius*	12.64	-20.11	BIO	90%		
30	PBM3267	Tennessee	on soil in cove hardwood forest	*Porpoloma umbrosum*	14.11	-26.92	BIO	100%		
31	RHP03958	Idaho	on litter in conifer forest	*Clavicorona taxophila*	-1.65	-22.13	SAP	99%		
32	SAT99-230-15	New Mexico	on soil in conifer forest	*Clavulinopsis corniculata*	12.62	-31.86	BIO	100%		
33	Marr3316	New York	on wood in mixed forest	*Ramariopsis lignicola*	15.84	-25.28	BIO	100%		
34	RHP4815	Oregon	on wood in conifer forest	*Mucronella flava*	-4.08	-21.01	SAP	100%		
35	STZ9976	Michigan	on soil in conifer forest	*Clavulinopsis* aff. *aurantiocinnabarina*	15.29	-27.05	BIO	100%		
36	RHP4070	Idaho	on soil in conifer forest	*Clavulinopsis gracillima*	12.63	-25.35	BIO	99%		

Table 5 Continued

No.	Specimen-voucher	Geographic location	Habitat	Species	δ15N (‰)	δ13C (‰)	Nutritional mode prediction	Prob.	δ15N analytical SE	δ13C analytical SE
37	RHP4116	Idaho	on soil in conifer forest	*Clavulinopsis umbrinella*	14.57	-23.75	BIO	100%		
38	Ceska11-04-10	British Columbia	on soil in lowland conifer forest	*Clavaria neonigrita*	7.99	-25.79	BIO	93%		
39	RHP4134	Idaho	on litter in conifer forest	*Clavicornona taxophila*	-2.68	-21.16	SAP	100%		
40	RHP3729	Idaho	on soil in conifer forest	*Ramariopsis crocea*	10.86	-23.39	BIO	100%		
41	STZ9846	Washington	on wood in lowland forest	*Mucronella alba*	-0.13	-19.73	SAP	100%		
42	JMB080409-11	Tennessee	on soil in cove hardwood forest	*Armillaria mellea*	0.31	-21.52	SAP	100%		
43	SAT09-213-07	Tennessee	on soil in cove hardwood forest	*Entoloma quadratum*	5.05	-25.5	BIO	95%		
44	JMB080609-01	Tennessee	on wood in Eastern Hemlock forest	*Tapinella atrotomentosa*	5.57	-20.04	SAP	100%		
45	JMB080409-98	Tennessee	on litter in cover hardwood forest	*Marasmius fulvoferrugineus*	3.04	-23.74	Equivocal	52%		
46	SAT09-216-15	Tennessee	on wood in Eastern Hemlock forest	*Gloeocantharellus purpurascens*	15.72	-25.34	BIO	100%		
47	ECV3996B	Tennessee	on wood in cove hardwood forest	*Galiella rufa*	-1.99	-26.11	BIO	65%		
48	BPL12	Tennessee	on soil in cove hardwood forest	*Catathelasma imperiale*	13.09	-24.48	BIO	100%		
49	SAT09-216-06	Tennessee	on litter in cove hardwood forest	*Psilocybe caerulipes*	-1.6	-23.29	SAP	93%		
50	PBM1856	Washington	on soil in montane conifer forest	*Cleistocybe vernalis*	1.11	-18.52	SAP	100%		

CHAPTER II
TESTING THE CORNER HYPOTHESIS OF FRUITING BODY EVOLUTION IN THE FAMILY CLAVARIACEAE (AGARICALES)

A version of this chapter is currently in review as:

Birkebak JM, Adamčík S, Matheny PB (in review) Testing the Corner hypothesis of fruiting body evolution in the family Clavariaceae (Agaricales). Molecular Phylogenetics and Evolution.

The dissertation writer performed a portion of the lab work, performed all analyses, and was the primary author of the manuscript.

Abstract

Evolution of fruiting body morphology has been suggested to drive patterns of diversity in the Agaricomycotina, a subphylum of primarily mushroom-forming fungi. Clavarioid (club-shaped) fruiting bodies have been hypothesized to be an important transitional state in the evolution of the agaricoid (lamellate-stipitate) fruiting body, the evolutionarily most successful fruiting body morphology. The genus *Camarophyllopsis* is a group of agaricoid fungi closely related to species producing clavarioid (club-shaped) fruiting bodies in the family Clavariaceae (Agaricales). Previous studies have suggested that species classified in the genus occur in two independent lineages, both of which are derived from clavarioid ancestors. This pattern of evolution would appear partially consistent with the Corner hypothesis of clavarioid ancestry. However, this hypothesis has not been explicitly tested using evolutionary analyses of robust, multilocus phylogentic reconstructions in any group of the Agaricomycotina. To do so, we reconstructed a multilocus phylogeny of the Clavariaceae and detected three independent groups of agaricoid fungi including the genera *Camarophyllopsis*, *Hodophilus*, and *Lamelloclavaria* gen. nov., which distinctly differ in their pileipellis structure. In addition, we find that the cantharelloid (pileate-nonlamellate) genus *Clavicorona* is derived within the paraphyletic clavarioid genus *Clavaria* and may represent a transitional state between clavarioid and agaricoid fruiting bodies, but agaricoid lineages are not observed to be derived from cantharelloid ancestors. Although an evolutionary bias has been shown toward production of agaricoid fruiting bodies in the Agaricomycotina, no support for an increase in diversification rate was detected in the Clavariaceae using Baysian Analysis of Macroevolutionary mixtures and Binary State Speciation and Extinction models. These are the first findings to strongly support transitions from clavarioid to agaricoid fruiting body morphologies and provide partial support for the Corner hypothesis. Alternative classifications for the genus *Clavaria* are discussed.

Introduction

The Agaricomycotina ia a subphylum of Basidiomycota characterized by a large diversity of fruiting body morphologies including resupinate, jelly-like, club and coral like, gastroid, cantharelloid, agaricoid and yeast-like forms. This

morphological diversity, however, is unequally distributed taxonomically with a sharp bias toward agaricoid (pileate-stipitate) forms that comprise ~60% (ca. 13,000) of the described species in the Agaricomycotina according to figures in the Dictionary of the Fungi (Kirk et al., 2008). The preponderance of agaricoid forms is found in the Agaricales, the most diverse order of the subphylum containing nearly half of the species (Hibbett, 2004; Hibbett and Thorn, 2001; Hibbett et al., 2014). It has been suggested that production of such complex fruiting bodies is a “driven” trend (McShea, 1994) with an asymmetric rate of transition by four to six orders of magnitude (Hibbett and Binder, 2002). Even when relatively under-sampled, the agaricoid and cantharelloid forms have been shown to be relatively stable morphological states (Hibbett, 2004). As one of the most successful trends in basidiomycete evolution, understanding the origins of the agaricoid form may be key to explain the disparity in morphological diversity in the Agaricomycotina.

Clavarioid (club-shaped, branched or not) fruiting body morphologies have been variously suggested as ancestral (Corner, 1970, 1972; Miller and Watling, 1987; Saville, 1955; Singer, 1986; Smith, 1971), derived (Arpin and Fiasson, 1971; Fiasson et al., 1970; Kreisel, 1969; Petersen, 1971), or independently evolved (Jülich, 1981). The Corner hypothesis of basidiomycete evolution was first put forward by Corner (1972) wherein he hypothesized that agaricoid fruiting body morphologies (pileate-stipitate-lamellate) are derived from species with clavarioid fruiting body morphologies with cantharelloid fruiting body morphologies (pileate-stipitate-nonlamellate) as a transitional state. Smith (1971) had previously postulated that in some cases agaricoid lineages evolved from clavarioid ancestors with cantharelloid intermediates. He gave the example of a seqeunce from *Clavariadelphus* Donk (clavarioid) to *Craterellus* Pers.: Fr. (cantharelloid) to *Cantharellus* Adans.: Fr. (cantharelloid) then to *Hygrophorus* Fr. (agaricoid). Pine et al. (1999) were the first to confirm that clavarioid fungi are polyphyletic and most closely related to fungi with non-clavarioid morphologies as hypothesized by many authors (e.g. Corner, 1970; Donk, 1964; Jülich, 1981). Hibbett (2004) showed that the clavarioid state is very labile with transitions to other forms being more frequent than in the reverse direction but only with moderate support (.10>p>.05). Some transitions between clavarioid to agaricoid or cantharelloid forms were detected, but this analysis did not discriminate among some states lumping, for example, agaricoid and cantharelloid together as a single state. As such, higher resolution is needed to test the Corner hypothesis. Clavarioid fungi make up only ~4% (approximately 800 species) according to figures in the Dictionary of the Fungi (Kirk et al., 2008), but this small percentage may be an important transitional state with respect to the evolution of additional forms.

A prior study on clavarioid fungi of the Clavariaceae Chevall. (Birkebak et al., 2013) demonstrated that two clades of agaricoid fruiting body producing lineages (*Camarophyllopsis* Herink and *Hodophilus* R. Heim) occur in the family and appear to have evolved agaricoid fruiting bodies independently from

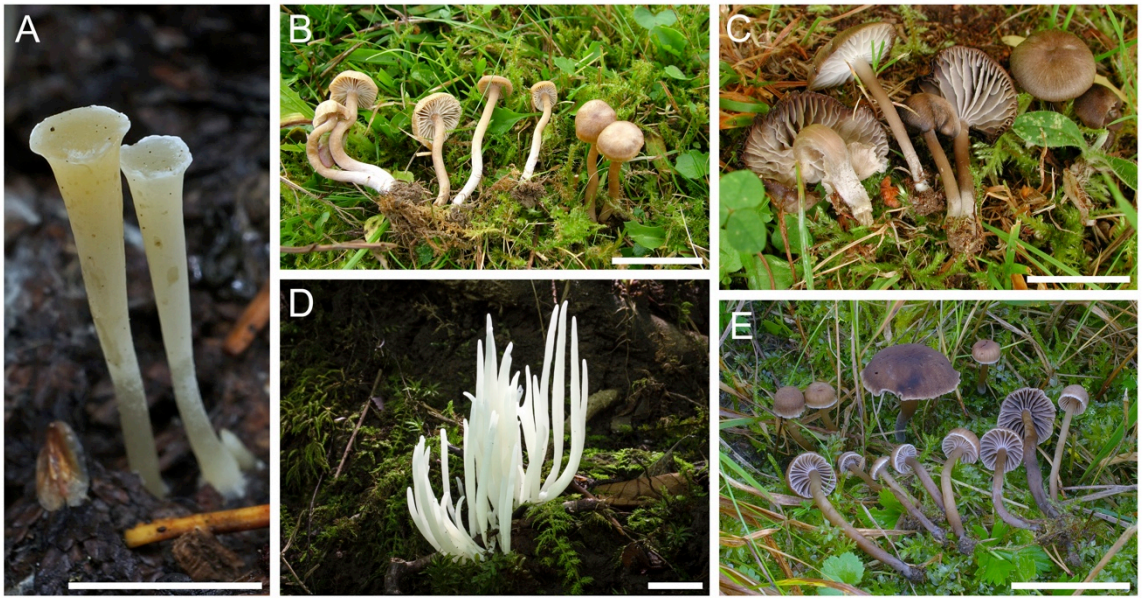

Figure 6. Diversity of fruiting body morphology in the crown group of the Clavariaceae. A. *Clavicorona taxophila* (photo: Sava Kristic). B. *Camarophyllopsis schulzeri* (Photo: Soňa Jančovičová). C. *Lamelloclavaria petersenii* (photo: Stefan Jacobsson). D. *Clavaria fragilis* group (photo: Mike Wood), E. *Hodophilus foetens* group (photo: Zuzana Egertová). Scale bars equal 1 cm.

clavarioid ancestors. However, sufficient statistical support was lacking to back this claim. To our knowledge this is the only preliminary support for the "*Clavaria* hypothesis" of basidiomycete evolution. Giachini et al. (2010) suggested that the production of coralloid fruiting bodies is an ancestral trait in the Gomphales from which cantharelloid taxa are derived. *Gloeocantharellus lateritius* (Petch) Corner, a species in the Gomphales described with lamellae, may represent a transition from a cantharelloid fruiting body producing species but this has not been investigated with molecular data. This could represent an intriguing variation on the "*Clavaria* hypothesis" whereby coralloid ancestors give rise to cantharelloid species, which in turn may give rise to agaricoid species.

The family Clavariaceae s.s. contains a diverse assemblage of fruiting body morphologies (Figure 6) in the genera *Clavaria* L.: Fr. (abbreviated *Cl.*), *Clavulinopsis* Overeem (*Cu.*), *Ramariopsis* (Donk) Corner (*R.*), *Mucronella* Fr. (*M.*), *Camarophyllopsis* Doty (*Cm.*), *Hyphodontiella* Å. Strid (*Hp.)*, and *Clavicorona* (*Cv.*) (Birkebak et al., 2013; Dentinger and McLaughlin, 2006; Larsson 2007; Matheny et al. 2006). Although traditionally classified in the Hygrophoraceae Lotsy, the agaricoid genus *Camarophyllopsis* has affinity with the Clavariaceae (Matheny et al., 2006) and was later shown to be nested within the genus *Clavaria* (Birkebak et al., 2013). In the latter publication, *Camarophyllopsis* was recovered in two separate clades, but resolution and

support were insufficient in this single gene study to reject the monophyly of *Camarophyllopsis*. The two clades recovered corresponded to *Camarophyllopsis* subgenus *Camarophyllopsis* and *Camarophyllopsis* subgenus *Hygrotrama* section *Hodophilus*, which can be separated based on structure of the pileus cuticle (pileipellis).

Also nested in *Clavaria* is the monotypic genus *Clavicorona*, which is unique in the family by producing fruiting bodies that are inflated upward, have a sterile upper surface but lack lamellar modification of the hymenium (fertile surface) and may represent a transitional state between clavarioid and agaricoid fruiting bodies. It is typically classified as a clavarioid genus (Corner, 1950; Dodd, 1972; Doty, 1947) but has a differentiated sterile upper surface, and thus, is better considered as producing cantharelloid fruiting bodies as its type species, *Craterellus taxophilus* Thom, was originally considered (Thom, 1904). Mature specimens also typically show some undulation or folding on the hymenium similar to many species of the cantharelloid genus *Craterellus*.

Intrigued by these findings we set out to study the genus *Camarophyllopsis* further with the following objectives: 1) produce a robust, well supported, multigene phylogeny to assess the taxonomic relationships between the genera *Clavaria, Clavicorona,* and *Camarophyllopsis* and test for their monophyly; 2) perform ancestral state reconstruction of fruiting body morphology to test the Corner hypothesis; 3) propose a new taxonomic arrangement based on these new evolutionary relationships; and 4) test whether transitions in fruiting body morphology are associated with shifts in diversification rate.

Materials and Methods

Taxon sampling

One-hundred and sixty-eight specimens in the *Clavaria-Camarophyllopsis-Clavicorona* clade, previously recovered in Birkebak et al. (2013), were sampled. Three regions (nLSU ribosomal RNA, ITS and *rpb2*) were analyzed in order to better clarify relationships between clades producing varying fruiting body morphologies (Table 7 in appendix). For Bayesian Analysis of Macroevolutionary Mixtures (BAMM) and Binary State Speciation and Extinction (BiSSE) models, an additional dataset was created adding all ITS environmental samples that BLAST most closely to the genera *Clavaria, Camarophyllopsis,* and *Clavicorona*. These sequence data (ITS) were extracted using the web-tool emerencia (Nilsson et al., 2005; Ryberg et al., 2009). Sequences with less than 70% coverage were excluded and all others were screened against chimerism.

DNA extraction, PCR, and Sequencing

The protocols of Birkebak et al. (2013) were followed for DNA extraction, PCR, and sequencing. The primer pairs ITS1F-ITS4 (Gardes and Bruns, 1993; White et al., 1990) were used to amplify the nITS region. Combinations of LR0R-LR7, LR0R-LR5, or LR0R-LR16

(http://sites.biology.duke.edu/fungi/mycolab/primers.htm) were used to amplify and sequence the nLSU region. The primer pair b6F and b7.1R (Matheny, 2005) were used to amplify and sequence the most variable region of the *rpb2* gene.

Phylogenetic analysis

Alignments for individual regions were created in CLUSTAL X (Larkin et al., 2007) and manually adjusted by eye in MacClade version 4.08 (Maddison and Maddison, 2005). Individual alignments were concatenated in SeaView version 4 (Gouy et al., 2010). Gblocks V0.91 (Castresana, 2000; Talavera and Castresana, 2007) was used to exclude ambiguously aligned sites. PartitionFinder (Lanfear et al., 2014) was used to identify the best partition scheme and molecular models under the AICc criterion. Maximum likelihood (ML) phylogenetic reconstruction was performed with RAxML version 7.4.2 (Stamatakis, 2006) implemented in RAxML GUI (Silvestro and Michalak, 2012) with 1000 bootstrap replicates. Bayesian inference (BI) was performed in MrBayes v3.2.2 (Ronquist et al., 2011) running 10,000,000 generations and sampling parameter states and trees every 10,000 generations. In order to ensure convergence had been reached, the average standard deviation of split frequencies was monitored to ensure it fell below .01 and trace files of all parameters were examined to ensure proper mixing. A 25% burn-in was used. Two species of *Clavulinopsis* and *Ramariopsis* each were used as outgroups based on Birkebak et al. (2013). The approximately unbiased test (AU test; Shimodaira, 2002) was performed in CONSEL (Shimodaira and Hasegawa, 2001) to evaluate competing tree topologies.

Divergence time estimation in BEAST

An absolute time-calibrated, birth-death chronogram was obtained using BEAST v2.2.0 (Bouckaert et al., 2014) following the guidelines of Heath (2014) using secondary calibrations from Ryberg and Matheny (2011) at the split between the Clavariaceae and the remainder of the Agaricales. The analysis was partitioned as above. Three independent searches were run for fifty million generations at which point all three converged at the same values as visualized in Tracer (Rambaut et al, 2014). All three runs were combined in LogCombiner with a 10 percent burnin and summarized in TreeAnnotator. Redundant infraspecific samples were pruned at a conservative age of up to 3.9 million years old. This high threshold may have resulted in lumping of species, but this can be accounted for by incorporating incomplete taxon sampling.

BAMM and BiSSE model testing

Bayesian Analysis of Macroevolutionary Models (BAMM; Rabosky, 2014) was used to assess if shifts in diversification rate could be detected across the chronogram particularly if associated with shifts in fruiting body morphology. Two independent BAMM analyses were run for fifty million generations using priors obtained from BAMMtools (Rabosky et al., 2014) and default parameters.

Outputs were analyzed in R (R core team, 2013) using BAMMtools with a 10% burnin. Convergence was assessed by checking effective sample size. Model comparisons were made by comparing Bayes factors. A 95% credible set of rate shift configurations was summarized in BAMMtools. Because there are no applicable estimates of species diversity given the revised taxonomy presented here, various levels of universal incomplete taxon sampling were evaluated increasing from 0% to 90% in 10% increments.

The genus *Camarophyllopsis* is estimated to contain 26 species, *Clavaria* 28 species, and *Clavicorona* as currently known is monophyletic (species counts from Kirk et al., 2008). Our taxon sample includes 20 OTUs of *Camarophyllopsis* s. l. (77% complete sampling), 71 of *Clavaria* (253%), and two of *Clavicorona* (200%; all estimates from Kirk et al., 2008). Given the differences in proportion of taxon sampling between traits (i.e. less than 100% taxon sampling of agaricoid members of the family while double or more for the other traits), analyses were run to test the effect of trait specific incomplete taxon sampling by increasing. In order to do this, the total estimate of agaricoid members (*Camarophyllopsis* s. l.) was increased by increments of ten addition species up to a total of 250% the current estimate of species diversity (Kirk et al., 2008).

Binary State Speciation and Extinction (BiSSE, Maddison et al., 2007) was used to assess if clades producing a pileus (cantharelloid and agaricoid) or lamellae (agaricoid) exhibited higher net diversification rates. The same chronogram was coded for presence/absence of these traits and run twice independently in BiSSE for 10,000 generations with the full model (unconstrained speciation, extinction, and transitions between states; best supported by likelihood ratio test). As there is currently no clade specific incomplete taxon sampling implemented in BiSSE, the effect of trait specific incomplete taxon sampling was tested by increasing the total estimate of *Camarophyllopsis* s. l. (agaricoid) species diversity by increments of 10 until reaching 250% of current diversity estimates.

Ancestral state reconstruction (ASR) analyses

Fruiting body morphology evolution was analyzed using ASR. The development of an agaricoid fruiting body is considered a process involving two separate steps: the development of a sterile upper surface (i.e. pileus) and the development of lamellae, and both characters are assessed separately. Clavarioid fruiting bodies do not produce a pileus or lamellae, cantharelloid fruiting bodies produce a sterile upper surface but no lamellae, and agaricoid fruiting bodies produce both. ML-ASR was performed on the most likely tree with BayesTraits (Pagel and Meade, 2007). BI-ASR was also performed with BayesTraits (Pagel and Meade, 2007) on 1000 randomly sampled trees from the posterior distribution of post burn-in trees generated by MrBayes.

Morphological examinations

Macromorphological descriptions were prepared from fresh material shortly after collection from the field. Color nomenclature standards follow Kornerup and Wanscher (1967). All micro-morphological characters were observed under the Olympus CX-41 light microscope with an oil-immersion lens at a magnification of 1000×. All drawings of microscopic structures, with the exception of spores, were made with a camera lucida using an Olympus U-DA drawing attachment at a projection scale of 2000×. Spores were scanned with an Artray Artcam 300MI camera and measured by Quick Micro Photo (version 2.1) software. Enlarged scanned pictures of spores were used for measuring with an accuracy of 0.1 µm and for making line drawings. Microscopic structures were examined on desiccated herbarium specimens in Congo red solution with ammonia after a short treatment in warm aqueous 10% KOH. Q-value is the length/width ratio of the spores. Measurements exclude ornamentation. Statistics for measurements of microscopic characters are based on 30 measurements and given as a mean value plus/minus standard deviation; values in parentheses give measured minimum or maximum values. Amyloidity and dextrinoidity of spores were tested in Melzer's reagent (Moser, 1978).

Results and Discussion

Phylogenetic reconstruction

BI and ML analyses yielded nearly identical phylogenetic reconstructions with only minor incongruences among a few short internodes. The BI tree is shown (Figure 7). Eight major clades and a single stem lineage can be identified in both reconstructions, all of which receive high support with the exception of the *Holocoryne* clade. Five clades are composed of species with clavarioid fruiting bodies traditionally classified in the genus *Clavaria* whereas two other clades and a single stem lineage contain agaricoid species exclusively.

One of the agaricoid clades corresponds to the genus *Camarophyllopsis* s. s. (*Camarophyllopsis* subgenus *Camarophyllopsis*) typified by *Hygrophorus schulzeri* Bres. The second agaricoid clade corresponds to *Hodophilus* (*Camarophyllopsis* subgenus *Hygrotrama* section *Hodophilus*) typified by *Hygrophorus foetens* W. Phillips. The single stem lineage is represented by a single collection that could not be identified as any published species or placed in any genus and is described below as new (*Lamelloclavaria petersenii*). AU tests on both phylogenetic reconstructions significantly reject the monophyly of *Camarophyllopsis* s. l. including the monophyly of all agaricoid species ($p<.01$). All three groups can be distinguished based on pileipellis morphology (Figure 8). The cantharelloid genus *Clavicorona* is found to be the earliest diverging lineage in the ingroup.The resulting clavarioid clades are not all well supported in their placement in either phylogenetic reconstructions. *Clavaria* s. s. (typified by *Cl. fragilis* Holmsk.: Fr.) is well supported as the sister group to *Camarophyllopsis* s. s. The *Cl. pullei* clade (containing species identified as *Cl. pullei* Donk and *Cl.*

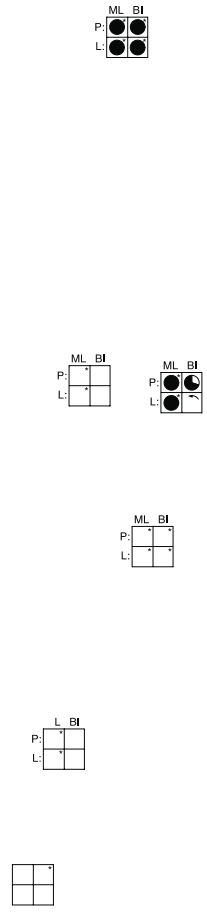

Figure 7. Bayesian majority rule consensus molecular phylogenetic reconstruction using the nITS, nLSU and rpb2 loci depicting relationships between agaricoid, cantharelloid, and agaricoid fruiting body producing species. Support values are indicated above the nodes as follows: Bayesian posterior probability/ML bootstrap value. If the topology was not present in the best ML tree, the space after the slash is left blank. Support values are only indicated for nodes with either a posterior probability at or above .90 or a bootstrap value above 60. The inferred ancestral state of fruiting body morphology is indicated with a pie chart for presence of a pileus (P) and lamellae (L). Black indicates probability of the absence of the trait, white indicates presence of the trait, an asterisk indicates a significant result. Legend: *Cl. = Clavaria, Cm. = Camarophyllopsis, Cu. = Clavulinopsis, Cv. = Clavicorona, H. = Hodophilus, R. = Ramariopsis.*

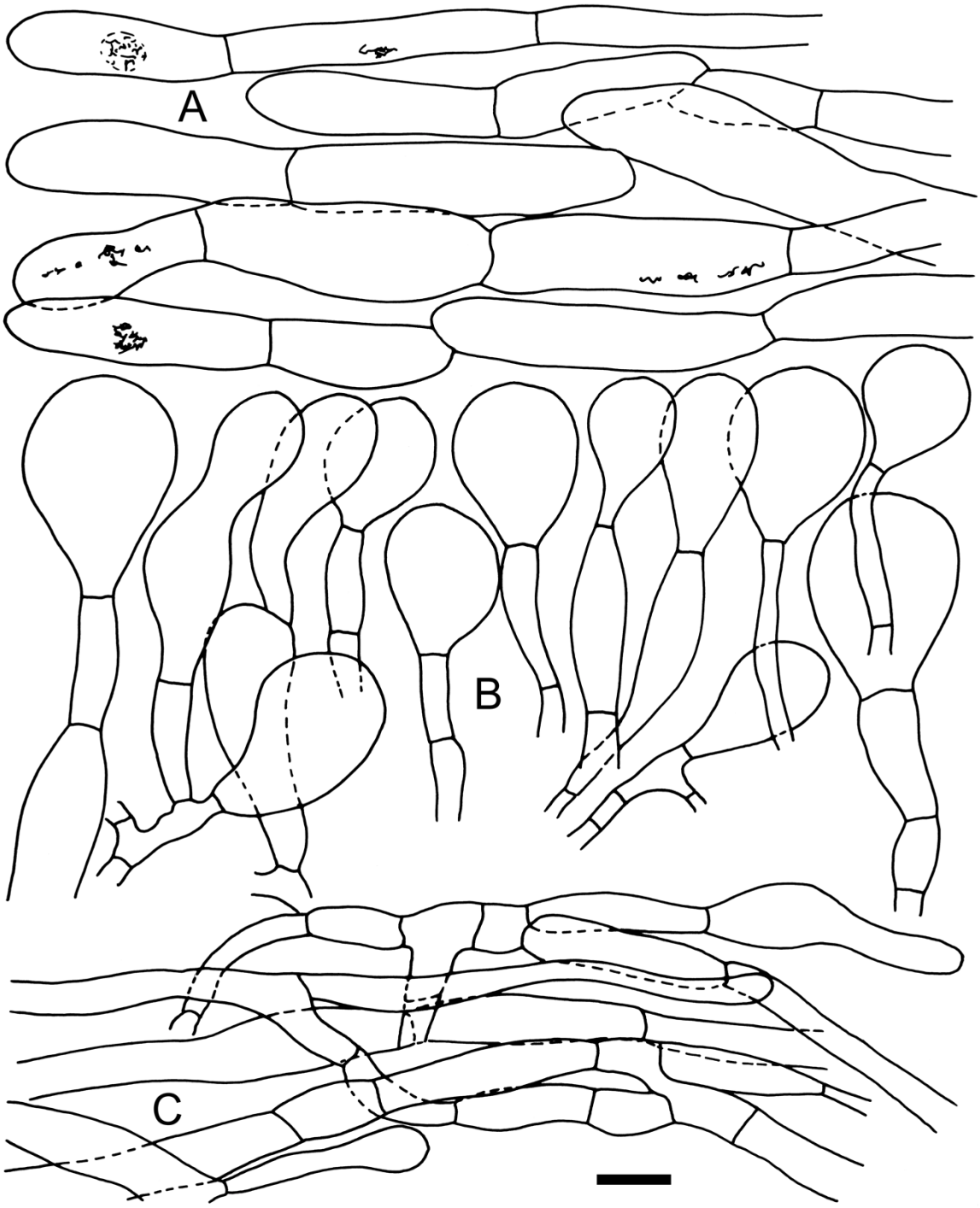

Figure 8. Comparison of pileipellis structure of different genera of lamellate Clavariaceae. A. Cutis of *Camarophyllopsis* with numerous repent hyphal terminations composed of chains of ellipsoid or cylindrical cells. B. Hymeniderm of *Hodophilus* with obpyriform or sphaeropedunculate hyphal terminations. C. Cutis of *Lamelloclavaria* with scattered hyphal terminations with frequent branching or anastomoses. Scale bar = 10 µm.

atroumbrina Corner) is sister to *Hodophilus*. The new genus *Lamelloclavaria* is found as the sister group to the *Cl. fumosa* clade (with *Cl. fumosa* Pers.: Fr. and *Cl. zollingeri* sensu auct.). A residual group of uncertain affinity (*Cl. atrofusca* clade) contains some darkly pigmented taxa. The *Holocoryne* clade does not receive high support but is composed of two well-supported subclades that are united by the presence of basidia that have a bifurcate base. This clade corresponds to the genus *Holocoryne* (Fr.) Bonord. typified by *Cl. falcata* Pers.: Fr. but the name has not been accepted at the rank of genus by most authors since its original elevation to generic rank in 1851 (Bonorden, 1951) and would require many new combinations. AU tests significantly reject the monophyly of *Clavaria* as currently circumscribed ($p<.01$). The genus *Clavaria* will need to be split into several genera reducing *Clavaria* s. s. to a small assemblage of species in the *Cl. fragilis* complex along with *Cl. rosea* Dalman ex Fr. Until the relationships of some of the residual clades currently considered in the genus can be resolved with robust support, no formal changes are proposed here.

Divergence time estimation of the Clavariaceae

The initial chronogram contained three hundred and thirty-seven tips but was reduced to ninety-three tips after pruning outgroups and intraspecific redundant sampling (Figure 9). Generally, similar phylogenetic relationships were recovered as in the BI and ML reconstructions above except along the already poorly supported backbone nodes and the placement of *C. fuscoferruginea* as sister to *Hodophilus* instead of the *C. pullei* clade and the placement of *Cv. taxophila* (with two cryptic lineages recovered) nested within the *Holocoryne* clade (Figure 9). None of these alternative placements received strong support. The ITS only environmental samples were placed within clades with high support but likely reduced the higher-level resolution of the phylogenetic reconstruction.

The Clavariaceae diverged from a common ancestor with the Agaricales between 98–195 mya (early Jurassic through the early Cretaceous, mean = 122 mya; Figure 9). The crown group, including the genera *Camarophyllopsis* s. l.*, Clavaria,* and *Clavicorona,* diverged 48–118 mya (early Cretaceous through the early Eocene, mean = 66 mya). The agaricoid and cantharelloid lineages diverged in the late Cretaceous at the earliest (< 100 mya) through the Oligocene at the very latest (Figure 9). *Clavicorona, Lamelloclavaria,* and *Camarophyllopsis* all diverged between the late Cretaceous through the late Eocene while *Hodophilus* diverged no earlier than the early Paleogene. The crown groups of *Camarophyllopsis* and *Hodophilus* split much earlier during the late Eocene to the Miocene.

BAMM and BiSSE diversification analyses

BAMM found no evidence of a significant shift in diversification across the chronogram. Additionally, there is significant evidence against a model involving one or more rate shifts (BF>5) though there is some rate heterogeneity across clades (Figure 10).

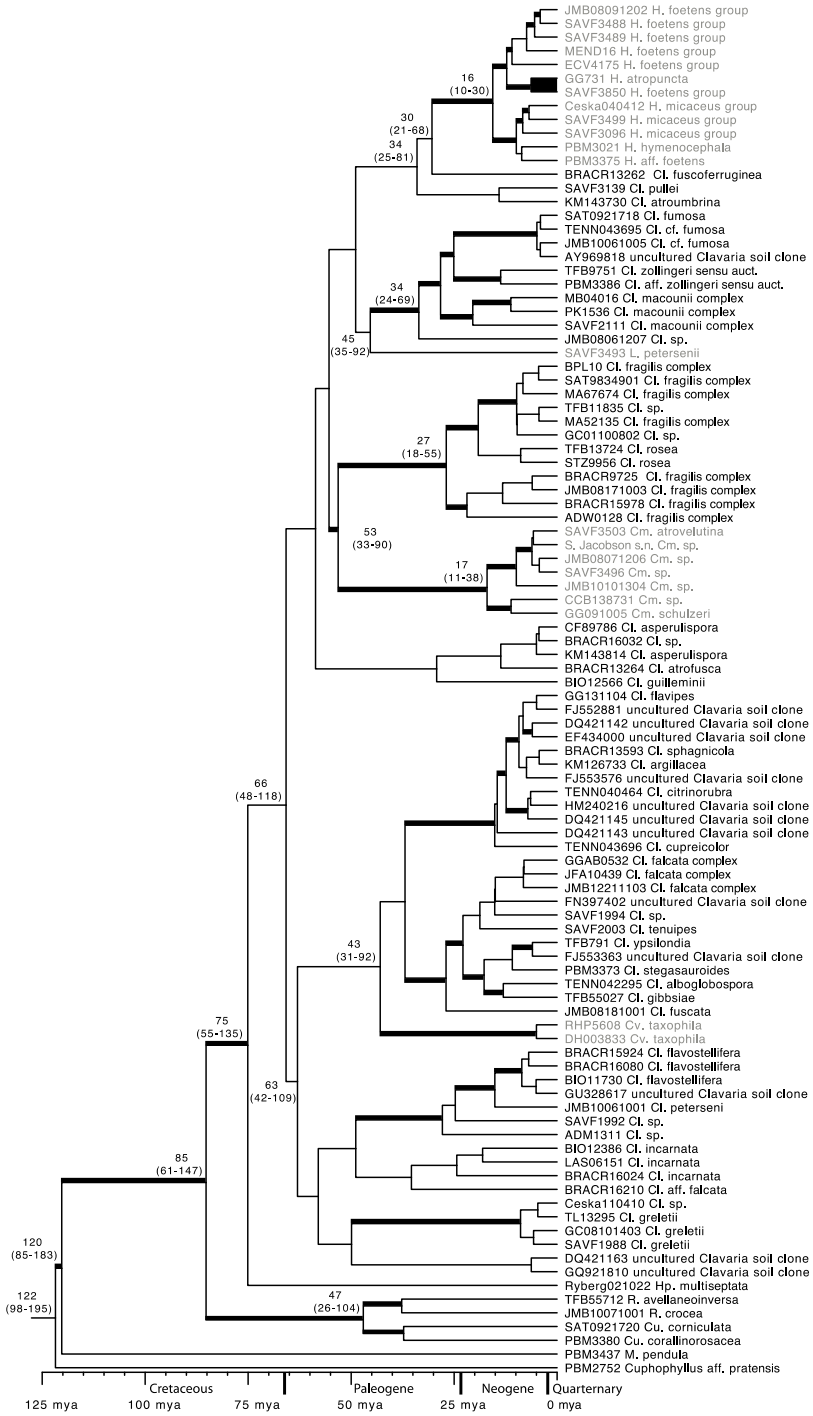

Figure 9. BEAST absolute time-calibrated chronogram of the expanded sampling matrix including ITS uncultured environmental samples obtained from GenBank. Thickened branched indicate >95% posterior probability. Node ages (with upper and lower 95% confidence intervals) are indicated above specific nodes. Abbreviations as in Figure 7 and Hp. = *Hyphodontiella*, M. = *Mucronella* in addition.

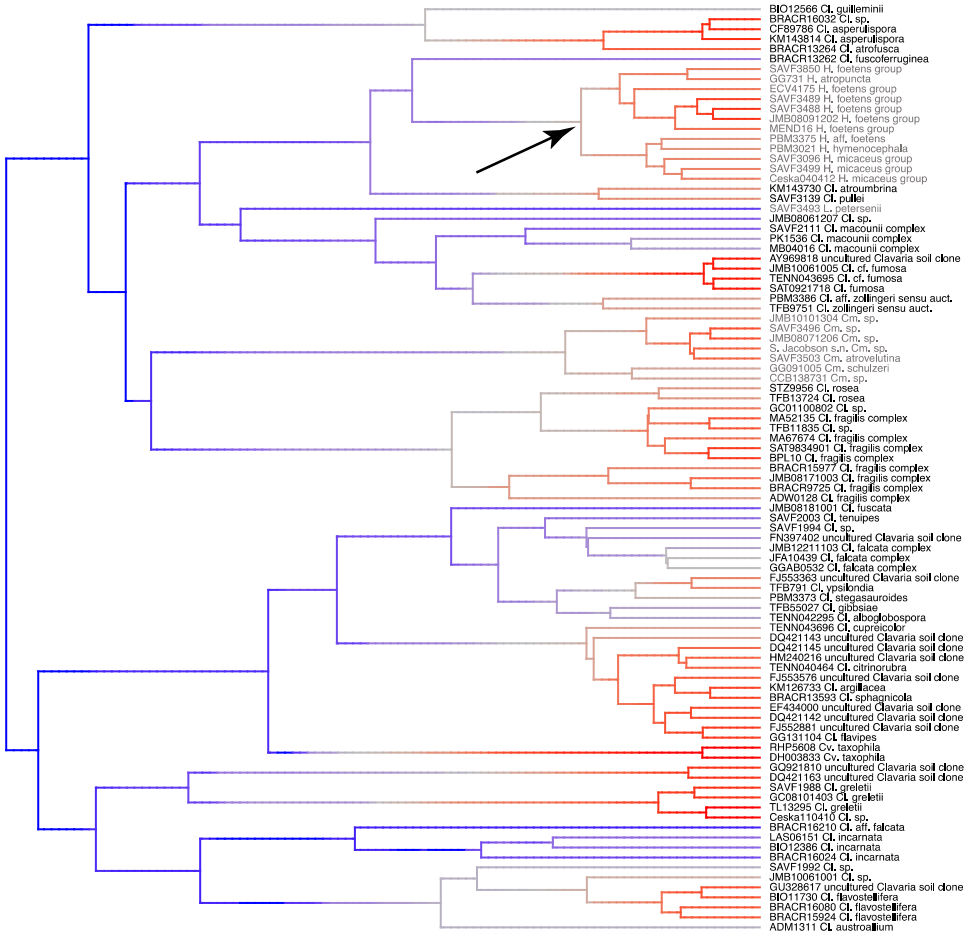

Figure 10. Mean phylorate plot from BAMM summarized by BAMMtools with heat indicating diversification rate (warm = fast, cold = slow). Lamellate lineages are in grey. The genus *Hodophilus* is indicated by an arrow showing the presence of a significant increase in diversification rate at 90% universal incomplete taxon sampling or < 42% lamellate specific incomplete taxon sampling bias.

Incomplete taxon sampling was not shown to affect the detection of a significant rate shift except in the most extreme case. One significant shift was detected on the branch leading up to the genus *Hodophilus* when incompletetaxon sampling was set to 90% only. A single rate model with no shifts was found to be the most supported model across all increments of incomplete taxon sampling but was not substantially more supported than alternative models except with 70% incomplete taxon sampling or less.

Trait specific incomplete taxon sampling was not shown to influence detection of rate shifts in BAMM up to an incomplete taxon sampling assignment of 42% for agaricoid species (nearly double the existing estimate). In these instances the same genus, *Hodophilus*, was found to show a small rate increase as found above with universal incomplete taxon sampling. Below 42% taxon sampling a single rate model was favored but lacked any substantial Bayes factor support.

While lineages with a pileus or lamellae were shown to be associated with slightly higher diversification rates overall in BiSSE (Figure 11), a significant increase was not detected except in the most extreme case of pileate incomplete taxon sampling (2.5x current agaricoid species estimate; Figure 11). Pileate and lamellate lineages were estimated to have very similar diversification rates and responded similarly to incomplete taxon sampling.

Ancestral state reconstruction and morphological evolution

Both ML- and BI-ASR ascribe a clavarioid fruiting body (smooth hymenium without a differentiated sterile upper surface) as the ancestral state for the Clavariaceae. ML-ASR supports three independent transitions to agaricoid fruiting bodies and one transition to a cantharelloid fruiting body from clavarioid ancestors (Figure 7). BI-ASR could not reject the possibility of a single transition to pileate (and subsequently lamellate) fruiting bodies with multiple reversions to clavarioid fruiting bodies (Table 6). Additionally there is strong conflict between the ML and BI trait reconstructions concerning the common ancestor of *Lamelloclavaria* and the *Cl. fumosa* clade with BI inferring an agaricoid common ancestor and a reversion to clavarioid ancestors. The genus *Clavicorona* exemplifies the transitional state between clavarioid and agaricoid fruiting body morphologies that would be necessary to give rise to the agaricoid genera in the family.

Taxonomy

Lamelloclavaria Birkebak & Adamčík gen. nov.

Mycobank No.: MB810134

Typus: *Lamelloclavaria petersenii* sp. nov.

Diagnosis: A genus in the family Clavariaceae producing agaricoid fruiting bodies

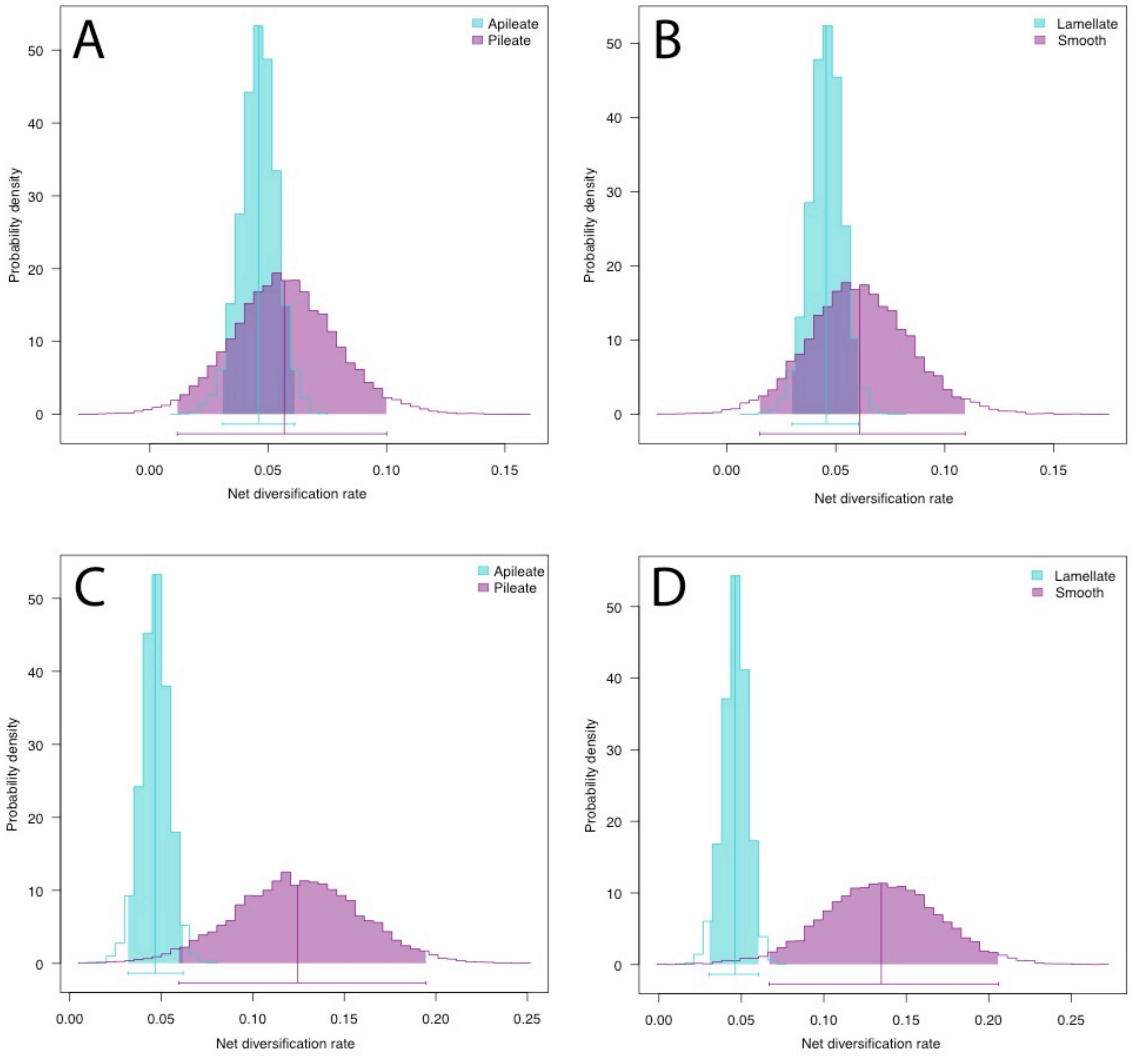

Figure 11. Probability density function showing means (vertical lines) and 95% confidence intervals (horizontal lines) of post burn-in estimates of trait specific diversification rates obtained in BiSSE. A. Pileate and apileate net diversification rates assuming complete taxon sampling. B. Lamellate and smooth hymenium net diversification rates assuming complete taxon sampling. C. Pileate and apileate net diversification rates with 31% incomplete taxon sampling of agaricoid members. D. Lamellate and smooth hymenium net diversification rates with 31% incomplete taxon sampling of agaricoid members.

Table 6. Maximum likelihood probabilities and Bayesian posterior probabilities for the ancestral state reconstruction of pileate and lamellate states for indicated nodes on the phylogeny as assessed in BayesTraits.

State (method)	root	ingroup	ingroup minus *Clavicorona*	ingroup minus *Holocoryne*	*Lamelloclavaria* plus fumosa clade	*Hodophilus* plus pullei clade	*Camarophyllopsis* plus *Clavaria*
Pileate (ML)	<.001	<.001	<.001	<.001	<.001	<.001	<.001
Pileate (Bayes)	<.001	0.26	0.3	0.3	>.999	0.3	<.001
Lamellate (ML)	<.001	<.001	<.001	<.001	<.001	<.001	<.001
Lamellate (Bayes)	<.001	0.03	0.32	0.32	>.999	0.32	<.001

similar to *Camarophyllopsis* and *Hodophilus* but with a rimulose nonhygrophanous pileus and a pileipellis that is a cutis. Basidiospores oblong, inamyloid, nondextrinoid, thin-walled, hyaline. Clamp connections absent in all tissues.

Lamelloclavaria petersenii Adamčík & Birkebak spec. nov., Figure 6C, 8C, 12

Mycobank No.: MB810135

Holotypus: Finland, Etelä-Häme Prov., Hyytiälä Forestry Field Station, on ground among the grass, near road margin, 61°50'47" N, 24°17'7.5" E, near *Acer pseudoplatanas*, *Betula* sp., *Populus tremula*, 6-Sept-2005, *S. Adamčík* (SAV F-3493).

Etymology: Generic name in reference to the phylogenetic relatedness to the genus *Clavaria* but distinct in producing pileate-lamellate fruiting bodies. Specific epithet in honor of Dr. Ronald H. Petersen who has contributed greatly to fungal systematics, taxonomy, and evolution of fruiting body morphology, with incredible contributions specifically to the Clavariaceae s. l.

Pileus 8–15 mm in diameter, first convex, later nearly planate, rarely slightly depressed, often with a small papilla at center, margin involute when young, becoming straight, nonstriate, surface nonhygrophanous, dry, finely rimulose, hair brown ((5E4), sepia brown (5F4), dark blond (5D3), to nougat brown (5D3), more or less uniformly colored. **Stipe** 16–20 × 1–2 mm, cylindrical, sometimes eccentric, smooth and shining, finely granulose near very apex, concolorous with the pileus, base sometimes white tomentose. **Lamellae** L=18–24, l=1–3, entirely adnate to slightly decurrent, edge entire, birch gray (5C2), dust grey (5D2), or drab (5E3), relatively thin. **Context** compact and elastic, pale grayish, becoming black, especially near and on the surface when dry, taste mild, lacking a

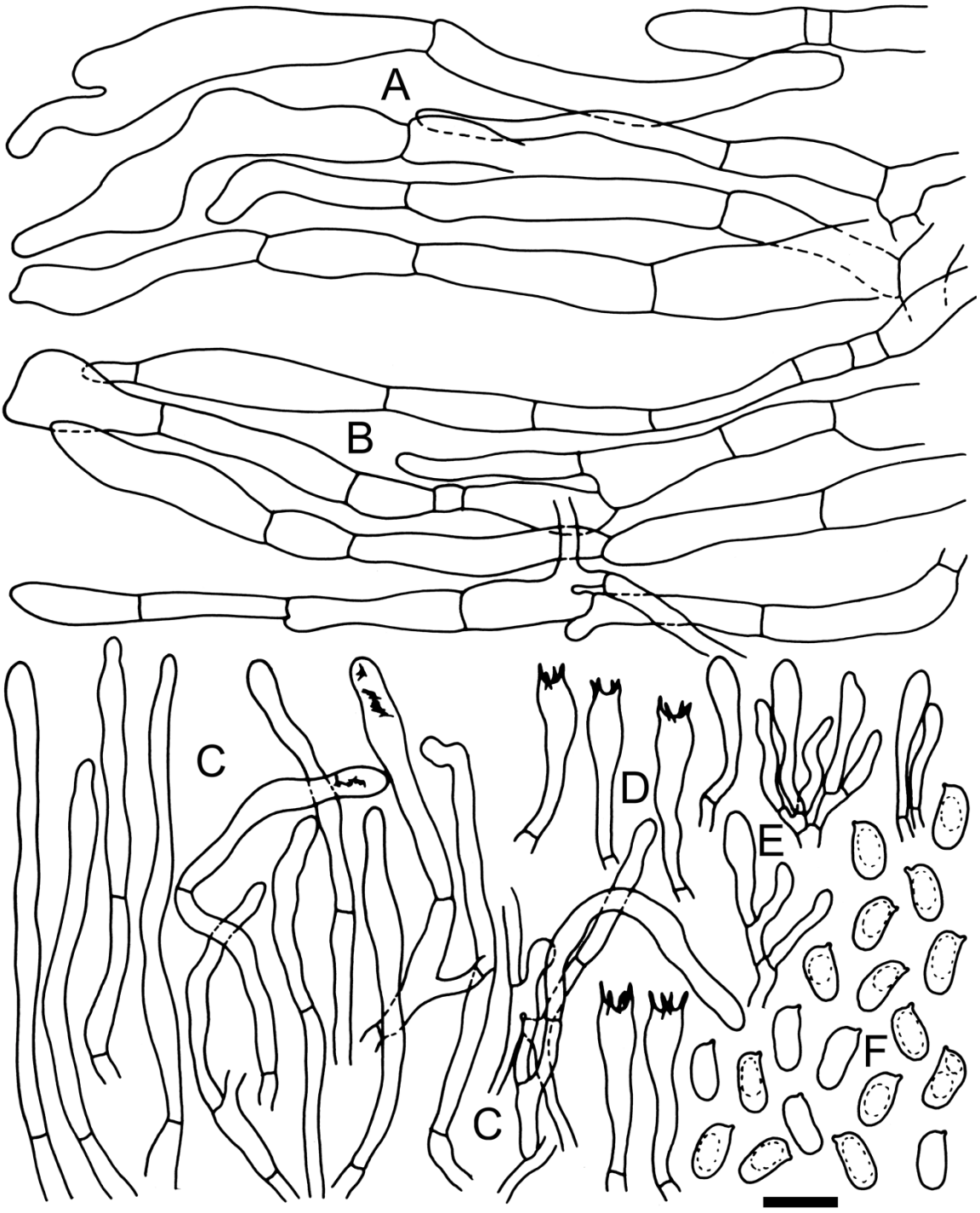

Figure 12. *Lamelloclavaria petersenii* (holotype). A. Hyphal terminations in pileipellis near the pileus center. B. Hyphal terminations in pileipellis near the pileus margin. C. Caulocystidia. D. Basidia. E. Basidiola. F. Spores. Scale bar = 10 µm, but only 5 µm for spores.

distinctive odor. **Spore deposit** not observed, most likely pale or white. **Spores** (5–)5.2–5.9(–6.2) × (2.5–)2.7–2.9(–3) µm, av. 5.5 × 2.8 µm, Q (length/width) = (1.83–)1.88–2.14(–2.35), av. Q = 2.01, phaseoliform to oblong, sometimes with a central constriction, hyaline, smooth, inamyloid, not dextrinoid, usually with one large vacuole, thin-walled, hilar appendage 0.4–0.6 µm long. **Basidia** 4-spored, 22–26.5(–28) × 5–6 µm, av. 24.5 × 5.5 µm, hyaline, clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, 2–4.5 µm wide. **Hymenium** without cystidia, lamellae edge fertile and similar to hymenium on the sides. **Subhymenium** sharply delimited from a parallel hyphae of lamellae trama, pseudoparenchymatic, ca. 10–15 µm deep, trama of the lamellae composed of parallel, ca. 3–10 µm wide, hyphae that are often anastomosed and sparsely branched, often with very short cells (ca. 10–25 µm), but sometimes also longer (50–100 µm long). **Pileipellis** near margin of the pileus a cutis, composed of relatively thin layer of relatively numerous, repent hyphal terminations with pale brownish intracellular pigment, terminal cells frequently larger, ventricose, fusiform, broadly clavate, to lageniform, occasionally narrow cylindrical, occasionally with irregular nodules, (6–)13.5–43(–78) × (3–)4.5–10(–13.5) µm, av. 28.4 × 7.5 µm; basal cells usually shorter and sometimes intermingled with very short small cells (shorter than 10 µm), with or without constrictions at the septa, usually forming chains of 2–4 (or more) unbranched cells; subpellis and trama of the pileus of ca. 5–12 µm wide, parallel, hyaline hyphae, that are very variable in length, usually shorter than 50 µm and intermingled with very short (up to 10 µm) elements, often anastomosed, scarcely branched. Hyphal terminations near center of the pileus also a cutis but of more dispersed and shorter hyphae, some composed of a single cell or lateral branch without a septum arising from horizontally oriented hyphae, with terminal cells more irregular and often nodulose, (13.5–)25.5–51(–66) × (2–)4–8(–10) µm, av. 38.2 × 5.9 µm, occasionally with intracellular crystals observed in Congo red. **Caulocystidia** dispersed or in small clusters, thin-walled, repent or ascending, with terminal cells measuring (14–)25–56(–69) × 2.5–4.5(–9) µm, av. 40.4 × 3.5 µm, typically narrow, moniliform and often flexuous, obtuse to slightly constricted near the apex, mostly cylindrical to narrowly clavate, with pale brownish intracellular pigments and occasionally with dispersed crystals visible in Congo red. Trama of stipe of comparatively wider hyphae than caulocystidia, often thick walled but otherwise similar to those in the pileus trama. **Clamp connections** absent in all tissues.

Note: The designation of the genus *Lamelloclavaria* is based on the new species *L. petersenii*, which is based on a single collection made during the Nordic Mycological Congress 2005 in Finland. The collection of the type was observed in the field by a number of Scandinavian mycologists and subjected to discussion. It was immediately clear that it represents a rare and undescribed species. The combination of the broadly adnate to decurrent lamellae, white spore print, finely rimulose grey cap with a small papilla, absence of clamp

connections on hyphae and phaseoliform to oblong, small spores makes this species striking in the field and under the microscope. This genus is not treated in recent keys to agaricoid fungi occurring in Nordic countries (Knudsen and Vesterholt, 2012) and despite effort of the authors and other mycologists it has not been recollected during the last nine years. It would appear that we are dealing with an extremely rare but very conspicuous species. The genus is easily distinguished from other Clavariaceae by the pileipellis of cutis type (with repent dispersed hyphal terminations) and spore shape. The combination of the rimose pileus surface, small stature, and phylogenetic placement differentiate it from species in the Hygrophoraceae.

Hodophilus R. Heim ex R. Heim, Rev. Mycol. 30: 231 (1966)

≡ *Hodophilus* R. Heim, Champignons d'Europe 2: 196 (1957) nom. inval. (Art. 39.1), nom. nudum

≡ *Camarophyllopsis* subgenus *Hygrotrama* section *Hodophilus* (R. Heim ex R. Heim) Arnolds, Mycotaxon 25: 642 (1986)

Typus: *Hygrophorus foetens* W. Phillips, Grevillea 7: 74 (1878)

Species:

Hodophilus foetens (W. Phillips) **Birkebak & Adamčík, comb. nov.** Basionym: *Hygrophorus foetens* W. Phillips, Grevillea 7: 74 (1878). Mycobank No.: MB810136

Hodophilus atropunctus (Pers.: Fr.) **Birkebak & Adamčík, comb. nov.** Basionym: *Agaricus atropunctus* Pers., Syn. Meth. Fung. 2: 353 (1801). Mycobank No.: MB810137

Hodophilus hymenocephalus (A.H. Sm. & Hesler) **Birkebak & Adamčík, comb. nov.** Basionym: *Hygrophorus hymenocephalus* A.H. Sm. & Hesler, Lloydia 5: 14 (1942). Mycobank No.: MB810138

Hodophilus micaceus (Berk. & Broome) **Birkebak & Adamčík, comb. nov.** Basionym: *Hygrophorus micaceus* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 5, 3: 207 (1879). Mycobank No.: MB810139

Note: This genus can be distinguished from *Camarophyllopsis* s.str. and *Lamelloclavaria* by the pileipellis that is composed of broadly inflated, globose, obpyriform to sphaeropendunculate terminal elements (Figure 8B) typically perpendicular to the pileus context (a hymeniderm). The four species recombined here are widely accepted and well known. Several more species will likely be transferred from *Camarophyllopsis* to this genus based on pileipellis morphology but are awaiting morphological study and DNA sequencing to determine their exact placement.

Nomenclatural note: R. Heim (1966) published several invalid combinations as they lacked citation of a basionym. These and one additional combination are made above.

Camarophyllopsis Herink, Sborn. Severocesk. Musea, Prir. Vedy 1: 61 (1958)

Typus: *Hygrophorus schulzeri* Bres., Fungi Tridentini 4/5: 57 (1884)

Species:

Camarophyllopsis schulzeri (Bres.) Herink, Sborn. Severocesk. Musea, Prir. Vedy 1: 62 (1958)

Camarophyllopsis atrovelutina (Romagn.) Argaud, Doc. Mycol. 31: 47 (2002)

Camarophyllopsis deceptiva (A.H. Smith & Hesler) Bon, Doc. Mycol. 26: 20 (1996)

This genus can be distinguished from *Hodophilus* and *Lamelloclavaria* by the pileipellis composed of chains of erect, ascending or repent, subcylindrical to ellipsoid end cells without distinctly inflated terminal elements (Figure 8A) There are likely more species in the genus than listed above but are awaiting detailed morphological study and DNA sequencing.

Conclusions

This study is the first to demonstrate evolutionary transitions in mushroom forming fungi from an ancestral clavarioid state to a derived agaricoid state. Three agaricoid lineages in the Clavariaceae represent separate genera that all share clavarioid ancestry. While no cantharelloid forms have been yet placed in a paraphyletic position with respect to agaricoid forms, it necessarily follows, by morphological constraint, that cantharelloid forms must be precursors to agaricoid forms (lamellae cannot form without a sterile upper surface creating an underside on which to form). These results are the first to support the Corner hypothesis of fruiting body evolution. Although there is a large bias in transitions to agaricoid fruiting bodies, there were no supported increases in diversification rates associated with agaricoid clades except in extreme cases of incomplete taxon sampling and trait specific incomplete taxon sampling bias. The family Clavariaceae is an ideal group for further investigation of the origins and transitions to agaricoid fruiting body morphologies (an incredibly successful evolutionary strategy in the Agaricomycotina) using experimental and genomic methods.

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Appendix

Table 7. Taxon sampling, specimen-voucher information, geographic location, sequence source, GenBank accession numbers for sequences used

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
Cm. atrovelutina	CL/F04.874 (LIP, split at TENN)	France: Nord-Pas-de-Calais: Arras: Nœux-lès-Auxi, réserve naturelle régionale	23-Nov-2004	C Lécuru	JM Birkebak	This study	KP257172			
Cm. atrovelutina	JMB10071301 (TENN)	USA: Tennessee: Cambell County: Norris Dam State Park, Anderson Ridge Trail	07-Oct-2013	JM Birkebak	JM Birkebak & S Adamčík	This study	KP257173		KP257246	
Cm. atrovelutina	SAV F-3503 (SAV)	Slovakia: Krivoklát village: Biele Karpaty Mts., Krivoklátske lúky	31-July-2005	S Adamčík	S Adamčík	This study	KP257174	KP257097		
Cm. atrovelutina	SAV F-3504 (SAV)	Slovakia: Hostovice village: Laborecká vrchovina Mts., Hostovické lúky	18-Sept-2006	S Adamčík	S Adamčík	This study	KP257175	KP257098		
Cm. deceptiva	JMB10121301 (TENN)	USA: Tennessee: Cambell County: Norris Dam State Park, Andrews Ridge Trail	12-Oct-2013	JM Birkebak & S Adamčík	JM Birkebak & S Adamčík	This study	KP257176	KP257099	KP257247	
Cm. deceptiva	PBM3973 (TENN)	USA: Tennessee: Sevier County: Cherokee Orchard Loop, Rainbow Falls Trail	06-Sept-2013	PB Matheny	PB Matheny	This study	KP257177	KP257100	KP257248	
Cm. deceptiva	TENN024374 (TENN)	USA: North Carolina: Swain County: Deep Creek	19-July-1961	LR Hesler	LR Hesler & AH Smith	This study	KP257178	KP257101		Paratype
Cm. schulzeri	CL/F01.501 (LIP, split at TENN)	France: Pas-de-Calais	08-Sept-2001	A Flahaut	JM Birkebak	This study	KP257181	KP257102		
Cm. schulzeri	GG091005 (TENN)	United Kingdom: Wales: Gwynedd: Allt Goch	09-Oct-2005	G Griffith	G Griffith	Binder et al. 2010	EF537888		GU187819	
Cm. schulzeri	SAV F-3495 (SAV)	Slovakia: Osadné village, Laborecká highlands Mts., pastures near the village	11-Oct-2005	V Kučera	S Adamčík	This study	KP257182	KP257103		
Cm. schulzeri	SAV F-3500 (SAV)	Czech Republic: Mařenice village: Lužické hory Mts., Rozmoklá žába	07-Sept-2008	Z Egertová	S Adamčík	This study	KP257183	KP257104		
Cm. sp.	CCB138731 (TENN)	USA: Tennessee: Loudon County: Greenback	05-July-2013	CC Braaten	JM Birkebak	This study	KP257179			

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
Cm. sp.	ECV5505 (TENN067613)	USA: Tennessee: Sevier County: Greenbrier, trail to cemetary	06-Aug-2012	EC Vellinga	JM Birkebak	This study	KP257180			
Cm. sp.	JMB08071206 (TENN067423)	USA: Tennessee: Blount County: Cades Cove, first bridge on Forge Creek Road	07-Aug-2012	JM Birkebak	JM Birkebak	This study	KP257184	KP257105	KP257249	
Cm. sp.	JMB10101304 (TENN)	USA: Tennessee: Cambell County: Norris Dam State Park, Andrews Ridge Trail	10-Oct-2013	JM Birkebak	JM Birkebak & S Adamčík	This study	KP257185	KP257107	KP257250	
Cm. sp.	SAV F-3496 (SAV)	Slovakia: Svetlice village: Biele Karpaty Mts., pasture near the village	21-Sept-2006	V Kučera	S Adamčík	This study	KP257186	KP257106		
Cm. sp.	S. Jacobsson 3453 (H)	Finland				Saar et al. unpublished	AM946415			as *Cm. schulzeri* in GenBank
C. alboglobospora	TENN042295 (TENN)	New Zealand: Northland: Kaitui Kaipara: Waipoua Reserve	23-June-1981	RH Petersen & AH Smith	RH Petersen	This study	HQ877682			Holotype
C. argillacea	TFB10710 (TENN058796)	Greenland: Qeqqata: Sisimiut: end of road behind village	18-Aug-2000	C Cripps	RH Petersen	This study (ITS) Birkebak et al. 2013 (LSU),	HQ877683	KP257108		
C. argillacea	ELj98 (GB)	Sweden				Larrson et al. 2004	AY463395			
C. argillacea	BRA CR16025 (BRA)	Slovakia: Záhorie	18-Oct-2008	V Kautman	Kautmanová	Kautmanová et al. 2012	JQ415930			
C. argillacea	K(M)126733	United Kingdom: Surrey: Fairmile	03-Nov-2004	EM Brown, BM Spooner		Kautmanová et al. 2012	JQ415931			
C. asperulispora	C(F)89786	Sweden: Uppland: Uppsala County: Predikstolen	30-Aug-1988	J Nitare	J Nitare	Kautmanová et al. 2012	JN315791			as *Cl. asperulospora* in GenBank
C. asperulispora	K(M)143814	United Kingdom: West Lancachire, Eaves Woods	16-Oct-2006	J & S Weir	P Roberts	Kautmanová et al. 2012	JN315790			as *Cl. asperulospora* in GenBank
C. atrofusca	BRA CR13264 (BRA)	Norway: Skrattasen: Steinkjer	05-Sept-2009	V Kučera	I Kautmanová	Kautmanová et al. 2012	JN315785			

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. atroumbrina	K(M)143730	United Kingdom	24-Oct-2006	SE Evans	I Kautmanová	Kautmanová et al. 2012	JN315792			
C. atroumbrina	BRA CR13265 (BRA)	Norway: Akershus, Nesodden, Roer	06-Sept-2009	V Kučera	I Kautmanová	Kautmanová et al. 2012	JN315786			
C. atroumbrina	BRA CR13271(BRA)	Norway: Buskerud: Nedre Eiker, Ryghsettra	11-Sept-2009	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JN315787			
C. citrinorubra	TENN040464 (TENN)	Australia: New South Wales: Royal National Park, causeway below Waterfall Station	08-June-1977	RH Petersen	RH Petersen	Matheny & Wolfenbarger unpublished	HQ877686	HQ179661		Isotype
C. cupreicolor	TENN043696 (TENN)	New Zealand: Auckland: Huia Waitakere, Mill Bay	29-June-1981	E Horak	RH Petersen	This study	KP257187	KP257109		Paratype
C. echino-olivacea	TENN043686 (TENN)	New Zealand: Northland: Kaitui Kaipara: Waipoua Reserve near forestry headquarters	25-June-1981	RH Petersen	RH Petersen	This study	KP257188	KP257110		Holotype
C. falcata complex	BRA CR16666 (BRA)	Slovakia: Malužiná	01-Nov-2006	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415961			As *Cl. falcata* in GenBank
C. falcata complex	BRA CR16667 (BRA)	Slovakia: Hronec	19-Sept-2007	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415962			As *Cl. falcata* in GenBank
C. falcata complex	GGAB0532	United Kingdom: Wales: Aelybryn	23-Oct-2005	G Griffith	G Griffith	Kautmanová et al. 2012 (LSU), This study (ITS)	JQ415935	KP257111		As *Cl. falcata* in GenBank
C. falcata complex	SAV F-2011 (SAV)	Czech Republic, Orlické Hory Mts., kačerov	17-Oct-2008	S Adamčík		Kautmanová et al. 2012	GU299505			As *Cl. acuta* in GenBank
C. falcata complex	GC08101406	France: Tourbiere du Pinet	14-Oct-2008	G Corriol	I Kautmanová	Kautmanová et al. 2012	JQ415941			As *Cl. falcata* in GenBank
C. falcata complex	BRA CR16029 (BRA)	Slovakia: Muran, Predna Hora	10-Oct-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415940			As *Cl. falcata* in GenBank

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. falcata complex	CF32637	Denmark: Zealand: Klinteskov	11-Oct-1995	T Laessoe		Kautmanová et al. 2012	JQ415945			As *Cl. falcata* in GenBank
C. falcata complex	SAV F-1990 (SAV)	Slovakia: Hostovice village: Laborecká vrchovina Mts., Hostovické lúky	9-Oct-2005	S Adamčík		Kautmanová et al. 2012	GU299506			As *Cl. acuta* in GenBank
C. falcata complex	JFA10439 (WTU)	USA: Washington: Mason County: Pickering Road	12-Jan-1988	E Duffield	JM Birkebak	This study	KP257189	KP257112		
C. falcata complex	JFA10440 (WTU)	USA: Washington: Mason County: Pickering Road	28-Jan-1987	E Duffield	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877680	KP257113		As *Cl. acuta* in GenBank
C. falcata complex	MTS4577 (WTU)	Sweden: Smaaland: Hylte: Femsjo		MT Seidl	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877679	KP257114		As *Cl. acuta* in GenBank
C. falcata complex	JMB12211103 (TENN)	USA: Wahington: King County: Lincoln Park	21-Dec-2012	JM Birkebak	JM Birkebak	This study	KP257190	KP257115		
C. falcata complex	RHP4115 (TENN036662)	USA: Idaho: Boundary County: Upper Priest River area on Hughes Meadow road	30-Sept-1964	HV Smith	JM Birkebak	This study	KP257191	KP257116		
C. falcata complex	RHP3878 (TENN033742)	USA: Idaho: Boundary County: Upper Priest River area trail to Ruby Creek	14-Sept-1964	RH Petersen	RH Petersen	This study	KP257192	KP257117		
C. falcata complex	TFB55840 (TENN043602)	New Zealand: Northland: Kaitui Kaipara: Waipoua Reserve, Te Ngahere	31-May-1982	RH Petersen I	RH Petersen	This study	HQ877681	KP257118		As *Cl.* cf. *acuta* in GenBank
C. aff. falcata	BRA CR16210 (BRA)	Slovakia: Hybe	01-Sept-2007	Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415960			As *Cl.* aff. *acuta* in GenBank
C. flavipes	NH1 (UBC F14294)	Canada: British Columbia: Greater Vancouver Regionak District: Capilano Fish Hatchery	26-Oct-2002	N Haddad	JM Birkebak	Berbee et al. unpublished	AY228353	AY228353		as *Cl. acuta* in GenBank

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. flavipes	GG131104 (TENN063740)	United Kingdom: Wales: Gwynedd: Cnicht	13-Nov-2004	G Griffith	JM Birkebak	Matheny et al. unpublished (LSU) this study (ITS)	EF535267	KP257119		as *Cl. straminea* in GenBank
C. flavipes	BRA CR12770 (BRA)					Kautmanová et al. 2012	GU299507			
C. flavipes	BRA CR12809 (BRA)	Slovakia: Hybe	15-Aug-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415942			as *Cl. straminea* in GenBank
C. flavipes	BRA CR12808 (BRA)	Slovakia: Muráň, Predná Hora	10-Oct-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415943			as *Cl. straminea* in GenBank
C. flavipes	BRA CR12807 (BRA)	Slovakia: Muránska Zdychava	09-Oct-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415944			as *Cl. straminea* in GenBank
C. flavipes	CF44153	United Kingdom: Wales: Abergavenny	06-Nov-2005	J Vesterholt		Kautmanová et al. 2012	JQ415958			as *Cl. straminea* in GenBank
C. fragilis	BRA CR9726 (BRA)				I Kautmanová	Kautmanová et al. 2012	GU299500			Epitype
C. fragilis complex	AHS3657 (TENN033913)	USA: Idaho: Bonner County: Priest River Experimental Forest	16-Sept-1964	AH Smith	RH Petersen	This study	KP257193	KP257120		
C. fragilis complex	DL002867 (TENN033113)	USA: Washington: Grays Harbor: Sylvia State Park	30-Oct-1967	D Largent	D Largent	This study	KP257194			
C. fragilis complex	SAT9834901 (WTU)	USA: Wahington: King County: Seward Park	14-Dec-1994	SA Trudell	SA Trudell	Birkebak et al. 2013	HQ877688			as *Cl.* aff. *fragilis*
C. fragilis complex	MA59584 (MA)	Spain: Benamahoma	28-Nov-2003	A Castro		Kautmanová et al. 2012	JQ415951			as *Cl. fragilis* in GenBank
C. fragilis complex	MA62679 (MA)	Spain: Menorca: Snata Teresa	11-Dec-2004	B Mates		Kautmanová et al. 2012	JQ415952			as *Cl. fragilis* in GenBank
C. fragilis complex	MA67674 (MA)	Spain: Bertiz	11-June-2000	LM Garcia Bona		Kautmanová et al. 2012	JQ415954			as *Cl. fragilis* in GenBank

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. fragilis complex	DJM1262 (MINN)	USA: Minnesota: Fillmore County: Eagle Bluff Environmental Learning Center	22-Sept-2007	N Nebta		Dentinger & McLaughlin 2006	DQ284907			as *Cl. vermicularis* in GenBank
C. fragilis complex	RHP2899 (TENN033244)	USA: Washington: Island County: Whidbey Island	02-Nov-1967	D Largent	RH Petersen	This study	KP257195	KP257121		
C. fragilis complex	DAVFP10654 (TENN033581)	Canada: British Columbia: Capital Regional District: Saanich: Mount Douglas Park, West of Marine Drive	19-Jan-1958	WG Ziller	JM Birkebak	This study	KP257196			
C. fragilis complex	SAV F-1262 (SAV)	Slovakia: Biele Karpaty mts., Blažejová Natural Monument	30-Jul-2005	V. Kautman		Kautmanová et al. 2012	GU299501			as *Cl. fragilis* in GenBank
C. fragilis complex	BRA CR16017 (BRA)	Spain: Bilbao, Mundaka	15-Nov-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415933			as *Cl. fragilis* in GenBank
C. fragilis complex	BIO12389 (BIO)	Spain: Bilbao, Larrinagatxu	16-Oct-2007	I Olariaga	I Olariaga	Kautmanová et al. 2012	JQ415934			as *Cl. fragilis* in GenBank
C. fragilis complex	MA61797 (MA)	Spain: Goitiz, Bermeo	03-Dec-2004	I Olariaga	I Olariaga	Kautmanová et al. 2012	JQ415949			as *Cl. fragilis* in GenBank
C. fragilis complex	MA67437 (MA)	Spain: Elizondo	01-Nov-1991	LM Garcia Bona		Kautmanová et al. 2012	JQ415953			as *Cl. fragilis* in GenBank
C. fragilis complex	BPL10 (TENN)	USA: Tennessee: Morgan County: Frozen Head State Park	02-Oct-2010	BP Looney	JM Birkebak	This study	KP257197	KP257122	KP257251	
C. fragilis complex	JWL778 (WTU)	Michigan: Emmet County: Pellston		JW Lennox	JM Birkebak	This study	KP257198	KP257123		
C. fragilis complex	MA52135 (MA)	Spain: El Escorial	24-May-1998	G Moreno		Kautmanová et al. 2012	JQ415950			as *Cl. fragilis* in GenBank
C. fragilis complex	BRA CR9727 (BRA)					Kautmanová et al. 2012	GU299498			as *Cl. fragilis* in GenBank
C. fragilis complex	JMB08171003 (TENN)	USA: Tennessee: Blount County: Tremont	17-Aug-2010	JM Birkebak	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS, rpb2)	HQ877689	KP257124	KP257252	as *Cl.* aff.*fragilis* in GenBank

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. fragilis complex	BRA CR9725 (BRA)					Kautmanová et al. 2012	GU299499			as *Cl. fragilis* in GenBank
C. fragilis complex	BRA CR15978 (BRA)	Spain: Bilbao, Mundaka	15-Nov-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415932			as *Cl. fragilis* in GenBank
C. fragilis complex	ADW0128 (TENN064092)	USA: Tennessee: Cocke County: Cosby	28-June-2009	AD Wolfenbarger	JM Birkebak	Birkebak et al. 2013	HQ877687			as *Cl.* aff.*fragilis* in GenBank
C. fumosa	BRA CR15656 (BRA)	Slovakia: Zuberec: Mačie diery Nature Reserve	16-July-2007	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JN315795			
C. fumosa	BRA CR15655 (BRA)	Slovakia: Malužiná village, Michalovo valley	09-Sept-2006	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JN315796			
C. fumosa	BRA CR748 (BRA)	Slovakia: Malužiná village, Michalovo valley	30-Aug-2010			Kautmanová et al. 2012	JN315798			
C. fumosa	GG151003 (TENN063541)	United Kingdom: Wales: Powys: Epynt	05-Oct-2003	G Griffith	G Griffith	Matheny et al. unpublished	EF535268	KP257125		
C. fumosa	MR00170 (TENN064094)	USA: Tennessee: Blount County: Elkmont, Jake's Creek Trail	04-Aug-2009	KM Ryberg	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877696	JN214482		as *Cl.* cf. *rubicundula* in GenBank
C. fumosa	SAT0921718 (TENN064091)	USA: Tennessee: Cocke County: Cosby	05-Aug-2009	SA Trudell	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877695	JN214483		as *Cl.* cf. *rubicundula* in GenBank
C. fumosa	TFB11839 (TENN060724)	Russia: Primorsky Krai: Khasanksy: Kedrovaya Reserve	17-Aug-2005	RH Petersen	RH Petersen	This study	KP257199	KP257126		
C. cf fumosa	JMB10061005 (TENN065659)	USA: Tennessee: Sevier County: Greenbrier	06-Oct-2010	JM Birkebak	JM Birkebak	Birkebak et al. 2013 (LSU)	HQ877690			as *Cl.* cf. *rubicundula* in GenBank

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. cf fumosa	TENN043695 (TENN)	New Zealand: Northland: Kaitui Kaipara: Waipoua Reserve	24-June-1981	RH Petersen	RH Petersen	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877697	KP257127		as *Cl.* cf. *rubicundula* in GenBank
C. fuscata	JMB08181001 (TENN)	USA: Tennessee, Sevier Co., Rainbow Falls Trail	18-Aug-2010	JM Birkebak	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS, rpb2)	HQ877691	KP257128	KP257253	
C. fuscoferruginea	BRA CR13262 (BRA)	Norway: Buskerud: Nedre Eiker, Ryghsettra	11-Sept-2009	V Kautman	I Kautmanová	Kautmanová et al. 2012	JN315784			
C. gibbsiae	TFB55027 (TENN043551)	New Zealand: Tasman: Murchison: 6.5 km from six-mile crek	11-May-1982	RH Petersen	RH Petersen	This study	KP257200	KP257129		
C. globospora	TFB55980 (TENN045945)	USA: Washington: Whatcom County: Thompson Creek Road near Mount Baker	11-Oct-1984	L Farwell	RH Petersen	This study	KP257201	KP257130		
C. greletii	TL-13295	Denmark: Sjaelland, Rosanaes	07-Oct-2007	T Lassoe	I Kautmanová	Kautmanová et al. 2012	JN416778			
C. greletii	SAV F-1988 (SAV)	Slovakia: Hostovice village, Hostovické lúky	09-Oct-2005	S. Adamčík	S. Adamčík	Kautmanová et al. 2012	GU299504			
C. greletii	K(M)143840	United Kingdom: Leicestershire, Ashby de la Zouch, New Lount Nature Reserve	07-Oct-2006			Kautmanová et al. 2012	GU299503			
C. greletii	GC08101403	France: Aude, Roquefeille, Tourbiere du Pinet	14-Oct-2008	G Corriol		Kautmanová et al. 2012	GU299502			
C. guilleminii	BIO12566 (BIO)	Spain: Berastegi, Arteleku	12-Oct-2007	I Olariaga D	I Olariaga	Kautmanová et al. 2012	JQ415939			
C. incarnata	MA53113 (MA)	Spain: Tenerife, Anaga	22-Feb-2006	Dominguez		Kautmanová et al. 2012	JQ415948			
C. incarnata	BRA CR16030 (BRA)	Slovakia: Žilina, in city park	18-Oct-2008	L Jánošík		Kautmanová et al. 2012	JQ415937			

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. incarnata	BIO12386 (BIO)	Spain: Bilbao, Larrinagatxu	16-Oct-2007	I Olariaga	I Olariaga	Kautmanová et al. 2012	JQ415938			
C. incarnata	BRA CR16024 (BRA)	Slovakia: Hybe	15-Aug-2008	I Kautmanová	I Kautmanová	Kautmanová et al. 2012	JQ415936			
C. incarnata	LAS06/151 (GB0060436)	Sweden: Västra Götaland: Vanersborg: Rudet SV, Gundlebosjon N	08-Oct-2006	L & A Stridvall	L & A Stridvall	This study	KP257245			
C. macounii complex	PK1536 (UBC F13537)	Canada: British Columbia: Squamish-Lilloot Regional District: Lower Cheakamus River at beginning of canyon	25-Aug-1991	P Kroger	JM Birkebak	This study	KP257202	KP257131	KP257254	
C. macounii complex	MB04-016 (CUW)	USA: Rhode Island: Lincoln Woods State Park	07-Aug-2000	M Binder	JM Birkebak	Matheny et al 2007	DQ202267	AY745693	DQ385880	AFTOL-ID984 as *Cl. inaequalis* in GenBank
C. macounii complex	K(M)145803	United Kingdom: Wales: Llandybie	24-Oct-2006	PJ Roberts		Kautmanová et al. 2012	JQ415946			as *Cl. amoenoides* in GenBank
C. macounii complex	SAV F-2111 (SAV)	Estonia, Karnaki Isl.	23-Sep-2008	J Vesterhold		Kautmanová et al. 2012	GU299508			as *Cl. amoenoides* in GenBank
C. pullei	SAV F-3139 (SAV)	Czech Republic: Orlické Hory Mts., Uhřinov village	19-Oct-2008	S Valda	S Adamčík	This study	KP257203	KP257132	KP257255	
C. pullei	KGN98 (GB)	Sweden				Larsson et al. 2004	AY586646			Originally as *Cl. fumosa* in GenBank
C. pullei	BIO12378 (BIO)	Spain: Cordoba, Arroyo Pedroches	05-Dec-2003	I Olariaga	I Olariaga	Kautmanová et al. 2012	JN315794			
C. pullei	GC02092801	France	28-Sept-2002	G Corriol	I Kautmanová	Kautmanová et al. 2012	JN315797			
C. pullei	GC99102304	France	23-Oct-1999	G Corriol	I Kautmanová	Kautmanová et al. 2012	JN315793			
C. redoleoalii	DJM1079 (MINN)	New Zealand				Dentinger & McLaughlin (2006)	DQ284906			

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. rosea	STZ9958 (WTU)	USA: Michigan: Emmet County: Pellston Hills	27-June-1957	DA Stuntz	DA Stuntz	This study	KP257204			
C. rosea	Scott1 (TENN063100)	USA: Alaska: Kenai: Soldotna, Heritage Place Day Care Center	25-Aug-2009	S Scott	RH Petersen	This study	KP257205	KP257133	KP257256	
C. rosea	TFB13724 (TENN065117)	USA: Washington: Pend Oreille County: USFS Road 172 .5 miles off state road 31	July-2010	D Parker	D Parker	This study	KP257206	KP257134	KP257257	
C. rosea	K(M)135940	United Kingdom: Shropshire: Wyre Forest	21-Oct-2005	R Winmall		Kautmanová et al. 2012	JQ415928			
C. rosea	CF26590	Denmark: Hodrjylland: Hostermark	22-June-1995	S Hansen		Kautmanová et al. 2012	JQ415929			
C. sp.	Ceska110410 (UBC)	Canada: British Columbia: Capital Regional District: John Dean Provincial Park, Slektain Trail	03-Nov-2004	A & O Ceska	A & O Ceska	This study	KP257207	KP257135		
C. sp.	TFB11835 (TENN060720)	Russia: Primorsky Krai: Khasanksy: Kedrovaya Reserve	17-Aug-2005	RH Petersen		This study	KP257208	KP257136	KP257258	
C. sp.	GC01100802	France: Cessey	08-Oct-2001	G Corriol		Kautmanová et al. 2012	JQ415956			
C. sp.	JMB08061207 (TENN)	USA: Tennessee: Sevier County: Greenbrier, trail to cemetary	06-Aug-2012	JM Birkebak		This study	KP257209	KP257137	KP257259	
C. sp.	SAV F-1994 (SAV)	Slovakia: Zliechov, Strážov valley	07-Oct-2005	S Adamčík		Kautmanová et al. 2012	JQ415963			
C. sp.	ADM1311 (TENN051311)	Brazil: Parana	27-June-1989	A de Meijer		Birkebak et al. 2013 (LSU), This study (ITS)	HQ877685	KP257138		as *Cl. australiana*
C. sp.	JMB10061001 (TENN065665)	USA: Tennessee: Sevier County: Greenbrier	06-Oct-2010	JM Birkebak		Birkebak et al. 2013 (LSU), This study (rpb2)	HQ877684		KP257260	

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
C. stegasauroides	PBM3373 (TENN)	Australia: Tasmania: Saint Columba Falls	21-May-2010	PB Matheny	JM Birkebak	Birkebak et al. 2013 (LSU), This study (rpb2)	HQ877698		KP257261	
C. subacuta	RHP2322 (TENN048438)	Japan: Tochigi: Nikko, near lake Chuzenjiko	27-Sept-1989	RH Petersen	RH Petersen	Birkebak et al. 2013 (LSU), This study (ITS)	HQ877699	KP257139		
C. ypsilondia	TFB791 (TENN042411)	New Zealand: Northland: Kaitui Kaipara: Waipoua Reserve near forestry headquarters	24-June-1981	RH Petersen	RH Petersen	This study	KP257210	KP257140	KP257262	Holotype
C. zollingeri sensu auct.	MA53142 (MA)	Norway: Akershus, Vestby	11-Aug-2002	P Perez Daniels		Kautmanová et al. 2012	JQ415955			as *Cl. zollingeri* in GenBank
C. zollingeri sensu auct.	JMB08040912 (TENN064095)	USA: Tennessee: Blount County: Elkmont	04-Aug-2009	JM Birkebak	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS, rpb2)	HQ877700	KP257141	KP257263	as *Cl. zollingeri* in GenBank
C. zollingeri sensu auct.	TFB9751 (TENN058652)	USA: Tennessee: Sevier County: Great Smoky Mountains National Park, Cherokee Orchard	07-July-2000	RH Petersen	RH Petersen	Matheny et al. unpublished	NG027629	AY854071	AY780940	AFTOL-ID 563 as *Cl. zollingeri* in GenBank
C. zollingeri sensu auct.	TFB11857 (TENN060741)	Russia: Primorsky Krai: Khasanksy: Kedrovaya Reserve	19-Aug-2005	A Psurtseva	RH Petersen	This study	KP257211	KP257142		as *Cl. zollingeri* in GenBank
C. aff. *zollingeri* sensu auct.	PBM3386 (TENN)	Australia: Tasmania: Break O'Day: Blue Tier Forest Reserve, Mount Michael Track	22-May-2010	PB Matheny	JM Birkebak	This study	KP257212	KP257143	KP257264	
Cu. coralinorosacea	PBM3380 (TENN)	Australia: Tasmania: Break O'Day: Blue Tier Forest Reserve, Goblin forest walk	22-May-2010	PB Matheny	JM Birkebak	Birkebak et al. 2013 (LSU), This study (ITS, rpb2)	HQ877707	KP257144	KP257265	

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
Cu. corniculata	SAT0921720 (TENN064106)	USA: Tennessee: Sevier County: Newfound Gap Trail	29-July-2009	SA Trudell	SA Trudell	Birkebak et al. 2013 (LSU), This study (ITS, rpb2)	HQ877713	KP257145	KP257266	
Cv. taxophila	TFB9186 (Danison672)	USA: California	20-Oct-1997	Danison	EB Lickey	Lickey et al. 2002	AF115333	AF115333		
Cv. taxophila	RHP5608 (TENN051926)	USA: Idaho: Shoshone County: Coeur D'Alene National Forest	24-Sept-1992	RH Petersen	RH Petersen	Birkebak et al. 2013	HQ877701			Epitype
Cv. taxophila	KBrothers s.n. (UBC F22826)	Canada: British Columbia: Squamish-Liloot Regional District: Whistler, Callaghan Valley	17-Oct-2010	K Brothers	K Brothers	This study	KP257213	KP257146		
Cv. taxophila	RHP3723 (TENN033965)	USA: Idaho: Boundary County: Upper Priest River area on Hughes Meadow road	19-Sept-1968	RH Petersen	RH Petersen	This study	KP257214			
Cv. taxophila	RHP3750 (TENN034002)	USA: Idaho: Boundary County: Upper Priest River area	21-Sept-1968	RH Petersen & AH Smith	RH Petersen	This study	KP257215			
Cv. taxophila	DH003833 (TENN034067)	USA: Idaho: Bonner County: Tule Bay on Priest Lake	23-Sept-1968	RH D Haywood	RH Petersen	This study	KP257216	KP257147		
H. atropuncta	GG731 (TENN063729)	United Kingdom: Wales: Powys: Welshpool: Powis Castle	22-Nov-2004	G Griffith	G Griffith	Matheny et al. unpublished	EF535270	KP257148		as *Cm. atropuncta* in GenBank
H. atropuncta	PAM10102001 (LIP, split at TENN)	France: Pas-de-Calais	20-Oct-2010	Paul Pinot	P Arthur-Moreau	This study	KP257217	KP257149	KP257267	
H. hymenocephalus	DJL95-081505 (TENN)	USA: North Carolina	15-Aug-2005	DJ Lodge	DJ Lodge	Matheny et al. 2006	DQ457679	DQ484066	DQ472726	AFTOL-ID 1892 as *Cm. hymenocephala* in GenBank
H. hymenocephalus	DJL98-081505 (TENN)	USA: North Carolina	15-Aug-2005	DJ Lodge	DJ Lodge	Matheny et al. unpublished	EF561628			as *Cm. hymenocephala* in GenBank
H. hymenocephalus	PBM3021 (TENN063784)	USA: Pennsylvania: Clinton County: Lock Haven University, Sieg Conference Center	10-Aug-2008	PB Matheny	PB Matheny	This study	KP257218		KP257268	
H. micaceus group	Ceska040412 (UBC)	Canada: British Columbia: Capital Regional District: Saanich: Tod Inlet	04-Apr-2012	A & O Ceska	JM Birkebak	This study	KP257219		KP257269	

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
H. micaceus group	Ceska041812 (UBC)	Canada: British Columbia: Capital Regional District: Saanich: Tod Inlet	18-Apr-2012	A & O Ceska	JM Birkebak	This study	KP257220	KP257150	KP257270	
H. micaceus group	CL/F04.103 (LIP, split at TENN)	France: Nord: Douai: Canal de la Sensée	15-Nov-2004	C Lécuru	JM Birkebak	This study	KP257221	KP257151		
H. micaceus group	LAS06/122 (GB0060375)	Sweden: Västra Götaland: Uddevalla: NR Ramseröd	07-Oct-2006	L & A Stridvall	JM Birkebak	This study	KP257222	KP257152		
H. micaceus group	PAM99082902 (LIP, split at TENN)	France: Haute-Savoie: Annecy: L'Etale, La Clusaz	29-Aug-1999	P Arthur-Moreau	JM Birkebak	This study	KP257223	KP257153		
H. micaceus group	PAM06091103 (LIP, split at TENN)	France: Pas-de-Calais: Calais: Forêt domaniale	11-Sept-2006	P Arthur-Moreau	JM Birkebak	This study	KP257224	KP257154		
H. micaceus group	SAV F-3096 (SAV)	Slovakia: Poľana Mts: Arborétum Borová hora	30-Sept-2009	I Kautmanová	S Adamčík	This study	KP257225			
H. micaceus group	SAV F-3499 (SAV)	Slovakia: Svetlice village, Biele Karpaty Mts., pasture near the village	31-July-2005	V Kučera	S Adamčík	This study	KP257226	KP257155		
H. micaceus group	SAV F-3505 (SAV)	Slovakia: Nová Bošáca village,Biele Karpaty Mts., trail to Veľký Lopeník hill	14-Oct-2010	K Devánová	S Adamčík	This study	KP257227	KP257156	KP257271	
H. foetens group	Ceska110301 (UBC)	Canada: British Columbia: Capital Regional District: Colwood: Royal roads University property	03-Feb-2001	A & O Ceska	A & O Ceska	This study	KP257228	KP257157	KP257272	
H. foetens group	ECV4175 (TENN065670)	USA: North Carolina: Haywood County: along Highway 32 near Big Creek	09-Oct-2010	EC Vellinga	JM Birkebak	This study	KP257229		KP257273	
H. foetens group	JMB10101301 (TENN)	USA: Tennessee: Cambell County: Norris Dam State Park, Andrews Ridge Trail	10-Oct-2013	JM Birkebak	JM Birkebak & S Adamčík	This Study	KP257230	KP257158	KP257274	
H. foetens group	JMB10121302 (TENN)	USA: Tennessee: Anderson County: Norris Dam State Park, Grist Mill trail	12-Oct-2013	JM Birkebak & S Adamčík	JM Birkebak & S Adamčík	This Study	KP257231	KP257159	KP257275	
H. foetens group	JMB10051302 (TENN)	USA: Tennessee: Monroe County: Cherokee National Forest, Walnut Grove Picnic Area	05-Oct-2013	JM Birkebak & S Adamčík	JM Birkebak & S Adamčík	This Study	KP257232		KP257276	

Table 7 Continued

Species	Specimen Voucher (Herbarium)	Geographic location	Date	Leg.	Det.	Sequence source	LSU Accession No.	ITS Accession No.	rpb2 Accession No.	Notes
H. foetens group	JMB10101302 (TENN)	USA: Tennessee: Anderson County: Norris Dam State Park, Grist Mill trail	10-Oct-2013	JM Birkebak & S Adamčík	JM Birkebak & S Adamčík	This Study	KP257233	KP257160	KP257277	
H. foetens group	PBM3930 (TENN)	USA: Tennessee: Blount County: 1.1 miles up Schoolhouse Gap trail	19-July-2013	PB Matheny	PB Matheny	This study	KP257234	KP257161	KP257278	
H. foetens group	JMB08091202 (TENN067461)	USA: North Carolina: Haywood County: Big Creek, at very beginning of Baxter Creek trail	09-Aug-2012	EC Vellinga	JM Birkebak	This study	KP257235	KP257162	KP257279	
H. foetens group	SAV F-3489 (SAV)	Slovakia: Nová Bošáca village, Biele karpaty Mts., Grúň Natural Monument	26-Sept-2005	S Adamčík	S Adamčík	This study	KP257236	KP257163		
H. foetens group	SAV F-3488 (SAV)	Slovakia: Závod village, Záhorská nížina lowland, Abrod Natural Reserve	30-Sept-2002	S Adamčík	S Adamčík	This study	KP257237	KP257164		
H. foetens group	SAV F-3497 (SAV)	Slovakia: Krivolát, Biele Karpaty Mts., Krivoklátske lúky	31-July-2005	S Adamčík	S Adamčík	This study	KP257238	KP257165		
H. foetens group	MEND16 (TENN)	USA: California: Mendocino County: Jackson State Forest off Highway 20	28-Jan-2012	D Smith	D Smith	This study	KP257239	KP257166	KP257280	
H. foetens group	JMB10251301 (TENN)	USA: Arkansas: Searcy County	25-Oct-2013	JM Birkebak & S Adamčík	JM Birkebak & S Adamčík	This study	KP257240	KP257167	KP257281	
H. foetens group	SAV F-3850 (SAV)	Slovakia: Oranská Polhora village, Oravské Beskydy Mts., Slaná voda	09-Oct-2012	N Rybáriková	S Adamčík	This study	KP257241	KP257168	KP257282	
H. foetens group	LAS06/123 (GB0060378)	Sweden: Västra Götaland: Uddevalla: NR Ramseröd	07-Oct-2006	L & A Stridvall	LSI	This study	KP257242	KP257169	KP257283	
H. aff. foetens	PBM3375 (TENN)	Australia: Tasmania: Break O'Day: Blue Tier Forest Reserve: Goblin forest walk	22-Apr-2010	F Karstedt	PB Matheny	This study	KP257243	KP257170	KP257284	
L. petersenii	SAV F-3493 (SAV)	Finland: Pirkanmaa: Juupajoki: Hyytiälä Forestry Field Station	06-Sept-2005	S Adamčík	S Adamčík	This study	KP257244	KP257171	KP257285	Holotype
R. avellaneo-inversa	TFB55712 (TENN043504)	New Zealand: Marlborough: Havelock: Pelorus Scenic Reserve	19-May-1982	RH Petersen	RH Petersen	This study	KP399950		KP399951	Holotype
R. crocea	JMB10071001 (TENN065661)	USA: Tennessee: Blount County: Elkmont	07-Oct-2010	JM Birkebak	JM Birkebak	Birkebak et al. 2013	HQ877715			

CHAPTER III
EFFECTS OF NUTRITIONAL MODE AND FRUITING BODY MORPHOLOGY ON DIVERSIFICATION IN TWO ECOLOGICALLY AND MORPHOLOGICALLY DIVERSE CLADES OF AGARICOMYCETES

The dissertation writer performed the majority of the lab work, performed all analyses, and was the primary author of the manuscript.

Abstract

The Agaricomycetes is the most diverse class in the kingdom Fungi and contains an incredible amount of ecological and morphological diversity. It is not currently known what traits promote diversification in this hyperdiverse clade of mushroom-forming fungi. The ectomycorrhizal (ECM) lifestyle has evolved many times independently across the Agaricomycetes from saprotrophic ancestors and is the nutritional mode of some of the most diverse genera of fungi. Here I test whether transitions to this novel lifestyle are associated with increased diversification rates. A high diversity of reproductive structure (fruiting body) morphology characterizes the Agaricomycetes. Different fruiting body morphologies are associated with large disparities in diversity but whether these are associated with differential diversification rates has not been tested. Here I test whether transitions in fruiting body morphology and hymenophore are associated with increased diversification rates. I created time calibrated phylogenetic reconstructions for two clades that contain both ecological and morphological diversity, the order Cantharellales and the family Clavariaceae (both containing similar suites of ecological and morphological diversity). Ancestral states were reconstructed in order to infer the number of transitions between traits. Binary and mulit-state speciation and extinction models were used to compare diversification rates associated with different ecological and morphological character states. A trait-independent Bayesian analysis of macroevolutionary mixtures model was used to assess whether shifts in diversification rates are associated with particular clades that correlate with character traits or if a single quickly evolving clade is driving the pattern seen with state speciation and extinction models. The ancestral states for both lineages were found to be saprotrophic with a smooth hymenophore but the fruiting body was found to be club-shaped in the Clavariaceae while resupinate in the Cantharellales. Biotrophic lineages were found to have a higher diversification rate in both clades. Lineages with more complex hymenophores were found to have faster diversification rates in most scenarios. Pileate and branched fruiting bodies were found to diversify faster than resupinate lineages in the Cantharellales but no effect of fruiting body on diversification rate was detected in the Clavariaceae. A significant rate shift was detected for or within the genus *Cantharellus*, the only lineage with a predominately wrinkled hymenophore, though the exclusion of the genus did not significantly alter the state-specific findings. One to three separate shifts were detected in the family Clavariaceae though not associated with any unique change in character state.

Introduction

The hyperdiverse Agaricomycetes is the largest class in the kingdom fungi with ~21,000 currently known species (~ 22% of known fungal diversity, Kirk et al. 2008). The class is host to a high level of morphological and ecological diversity (Hibbett et al. 2014) and contains a large number of saprotrophic and biotrophic lineages including parasites, mycorrhizal mutualists, lichens, and insect mutualists. Fruiting body morphology can be incredibly diverse ranging from jelly-like, resupinate, clavarioid, pileate-lateral, to pileate-stipitate. The hymenium can also be variously modified to increase the spore-producing area by production of pores, spines, wrinkles, or lamellae. Though the class is so ecologically and morphologically diverse, little is known about what nutritional modes, fruiting body morphologies, or hymenophores may contribute to this increased diversity.

The majority of the Agaricomycetes is composed of agaricoid (pileate-lamellate) species (approximately 75%, Hibbett 2004) and a transition bias by four to six orders of magnitude toward production of these fruiting bodies has been detected as an evolutionary trend (Hibbett and Binder 2002, Hibbet 2004). The ancestral state of the Agaricomycetes has been reconstructed as resupinate (Hibbett and Binder 2002) though this was not significantly supported in subsequent phylogenetic analyses (Hibbett 2004). Resupinate lineages are found in every order in the Agaricomycetes and are predominate in the early diverging lineages, including the Cantharellales (Binder et al. 2005, Larsson 2007, Larsson et al. 2004). The Agaricales (the largest order of Agaricomycetes), however, has the smallest fraction of resupinate species (Binder et al. 2005). Pine et al. (1999) have shown that clavarioid lineages (club shaped and branched) are highly polyphyletic and Hibbett (2004) has discovered that this morphology is highly labile with a high rate of transitions to other fruiting body morphologies and that transitions from pileate-stipitate to clavarioid fruiting bodies were near to nonexistent. Clavarioid fungi have represented a pivotal position in hypotheses concerning the evolution of complex fruiting body forms as ancestral, transitional, and derived (see Birkebak et al. in review for an overview).

Fisher & Money (2010) have illustrated that the production of lamellae increases the total available surface area for spore production by up to 20-fold. As lineages with lamellae, or other complex hymenophores, are found to be so speciose, this may suggest that these hymenophoral elaborations promote diversification. While the exact mechanism is not clear it could be that increased production of spores may lead to increases in offspring and geneflow that would reduce extinction rate. Whether these transitions are associated with increased diversification rates has never been tested.

The ectomycorrhizal (ECM) symbiosis involves a diverse assemblage of plant and fungal taxa. It has evolved independently approximately 80 times in the kingdom Fungi (37 times in the Agaricomycetes) and is distributed globally (Tedersoo 2010, Tedersoo & Smith 2013). In addition to the ECM symbiosis there are many other forms of mutualistic biotrophic interactions in the Agaricomycetes including lichenization and other, less understood, endophytic

interactions. While some of the largest genera in the Agaricomycetes are biotrophic (e.g. *Cortinarius* ca. 2000 species*, Russula* ca. 750, estimates from Kirk et al. 2008) others are very species depauperate (e.g. *Catathelasma* 4 species, *Multifurca* 5 species; estimates from Kirk et al. 2008). Lichenization has been shown to be associated with increased diversification rates in two lineages of Ascomycota but it is unclear whether other transitions to biotrophy increase diversification rates (Kraichak et al. 2015). Ryberg & Matheny (2011, 2012) found no support for slow downs in diversification rates in ECM clades in the Agaricales that would be indicative of historical radiations associated with the ECM lifestyle. They did not, however, compare rates of ECM lineages to related nonbiotrophic lineages. It has not been specifically tested whether switches in nutritional mode are associated with shifts in diversification rate.

New methodologies that have been recently developed that provide the means to explore correlations between traits and diversification rates. Bayesian Analysis of Macroevolutionary Mixtures (BAMM) takes a time-calibrated phylogenetic reconstruction and searches for trait-independent shifts in diversification along branches (Rabosky et al. 2013, Rabosky 2014). A benefit of this model is that there is no need to ascribe characters to a given clade in the model to test for rate shifts but it does not allow for comparison of diversification rates between traits. The Binary State Speciation and Extinction model (BiSSE; Maddison et al. 2007, FitzJohn et al. 2009) allows for comparison between the mean diversification rates associated with two traits. Its extension, the Multiple State Speciation and Extinction (MuSSE) model allows investigation of more than two states. These character state speciation and extinction models, however, do not perform well when taxon sampling is low (less than 300 tips) or when there is a high trait ratio biases exists (less than 10% of one character state; Davis et al. 2013). Furthermore BiSSE also may sometimes detect a significant association of neutrally evolving characters (Rabosky and Goldberg 2014). Care must also be taken to ensure that one does not ascribe a causal relationship between traits and diversification rates as non-coded traits may be driving patterns with which examined traits may be correlated.

Here I investigate the effects of transitions in morphology and nutritional mode in two ecologically and morphologically diverse clades: the family Clavariaceae (Agaricales) and the order Cantharellales (Figure 13). Both clades contain species that produce resupinate, clavarioid, and pileate-stipitate fruiting bodies with lamellate, hydnoid, poroid, wrinkled, and smooth hymenophores This morphological diversity makes these groups well suited to explore patterns of diversification with respect to fruiting body and hyemnial configuration. Birkebak et al. (in review) have found that transitions to pileate fruiting bodies or a lamellate hymenophore did not significantly increase diversification rates when investigating a subset of the Clavariaceae sampled here but this expanded sampling may lead to different results.

Figure 13. Morphological diversity in the family Clavariaceae and the order Cantharellales. A. Resupinate fruiting bodies produced by *Botryobasidium aureum* (Cantharellales; photo: Martin Livezy). B. Club-shaped (positively geotropic) fruting bodies produced by *Mucronella fusiformis* (Clavaraiceae; photo: Christian Schwarz). C. Resupinate fruiting bodies produced by *Tulasnella violea* (Cantharellales; photo: Mike Wood). D. Club-shaped fruiting bodies produce by *Clavaria rosea* (Clavariaceae; photo: Christian Schwarz). E. Pileate fruiting bodies with a smooth hymenophore produced by *Clavicorona taxophila* (Clavariaceae; photo: Drew Parker). F. Branched fruiting bodies produced by *Clavulina corraloides* group (Cantharellales; photo: Christian Schwarz). G. Pileate fruiting bodies with a wrinkled hymenophore produced by *Cantharellus formosus* (Cantharellales; photo: Noah Siegel). H. Pileate fruiting bodies with a smooth hymenophore produced by *Craterellus cornucopioides* (Cantharellales; photo: Christian Schwarz). I. Pileate fruiting bodies with a hydnoid hymenophore produced by *Hydnum repandum* (Cantharellales; photo: Noah Siegel). J. Pileate fruiting bodies with a lamellate hymenophore produced by *Hodophilus paupertinus* (Clavariaceae; photo: Christian Schwarz).

The order Cantharellales contains multiple ECM lineages and one lichenized genus (Moncalvo et al. 2006, Tedersoo et al. 2010). The families Ceratobasidiaceae and Tulasnellaceae have traditionally been considered saprotrophic but there is now strong evidence that some species in these families can form ECM symbioses with plants (Tedersoo et al. 2010). It is not currently known how many species can form these associations and whether they are obligate or facultative. Many lineages in the family Clavariaceae form a currently unknown or poorly understood biotrophic relationship with plants. Stable isotope signatures of carbon and nitrogen in the purportedly biotrophic Clavariaceae are found in the extreme range of biotrophic signatures (Birkebak et al 2014) along with a diverse assemblage of taxa including the Geoglossaceae and Hygrophoraceae p.p. (Seitzman et al. 2011). Some members of the Hygrophoraceae that exhibit these same extreme C and N isotope ratios have recently been implicated in endophytic, possibly vertically transmitted, associations with non-ECM plants (Halbwachs et al 2013a, b, Tello 2014) and the Clavariaceae may share a similar nutritional strategy.

Here I set out to test whether transitions in nutritional mode, fruiting body morphology, and hymenophore are associated with increases in diversification rates. Given observations on the patterns of diversity in the Agaricomycetes, I hypothesize that: 1) ECM or biotrophic lineages will exhibit increased diversification; 2) pileate lineages will exhibit increased diversification rates; and 3) lineages with complex hymenophores (increased spore production area: lamellate, wrinkled, or hydnoid) will exhibit increased diversification rates.

Materials and Methods

Datasets and alignments

Multilocus datasets were assembled from all nLSU, rpb2, tef1, and ITS sequences (Cantharellales; Table 10 in Appendix) or nLSU, nSSU, and rpb2 sequences (Clavariaceae; Table 11 in Appendix) from GenBank (Benson et al. 2011). Additional specimen-based sampling in the Clavariaceae was performed from herbarium specimens (deposited at TENN, WTU, SAV, GB, OSU, NY, UBC; Herbarium abbreviations as per Thiers [continuously updated]). Individual loci were aligned using MAFFT v 7 (Katoh & Standley 2013), misidentified and low coverage (<70%) sequences were manually pruned, ambiguously aligned regions were removed using Gblocks v 0.91b (Castresana 2000, Talavera & Castresana 2007), and were concatenated in Mesquite v 2.75 (Maddison & Maddison 2008). Partition finder v 1.1.1 (Lanfear et al. 2012, 2014) was used to identify the best partition scheme and models of molecular evolution. A preliminary phylogenetic reconstruction was run in raxmlGUI v 1.3.1 (Silvestro & Michalak 2012) in order to identify species level clades. All clades with a branch length of 0.02 or less were pruned down to a single representative with the highest locus number or sequence length coverage to eliminate species level redundancy. This arbitrary branch length was chosen based on differences

between well studied sister species though may have resulted in “lumping” of very closely related species, but incomplete taxon sampling in the subsequent diversification analyses should ameliorate this potential problem.

Absolute time-calibrated phylogenetic reconstructions

Absolute time calibrated phylogenies were reconstructed in BEAST2 v 2.2.0 (Bouckaert et al. 2014) using secondary calibrations from Ryberg & Matheny (2011). A Birth-Death model was used and priors were adjusted in accordance with the suggestions put forward by Heath (2015). The split between the Dacrymycetes and the Agaricomycetes and the split between the Cantharellales and the rest of the Agaricomycetes were used as calibration points for the Cantharellales dataset. Splits between the Clavariaceae and the rest of the Agaricales and the crown node of the Agaricomycetidae were used as calibration points for the Clavariaceae dataset. Three independent BEAST runs were performed and within and cross-run convergences were ensured by checking effective sample size using Tracer v 1.6 (Rambaut et al. 2014). Separate runs were combined in LogCombiner with a burn-in of 10-20% (depending on time to convergence of each specific run). TreeAnnotator was used to summarize a mean height chronogram from the post burn-in set of trees. Any clades with tips less than 3 million years old were pruned down to a single representative along with the outgroups.

Character coding

Trophic strategy was coded as biotrophic or saprotrophic for both datasets or additionally as ECM or non-ECM for the Cantharellales dataset. The Ceratobasidiaceae and Tulasnellaceae were coded as both biotrophic and ambiguous (BayesTraits) or as either in two separate BiSSE runs since there is currently no function to include ambiguous states. Fruiting body was coded as resupinate, club-shaped, branched or pileate. The resupinate genus *Hyphodontiella* (with only one taxon represented) was excluded from BiSSE analyses. Hymenophore was coded as smooth, hydnoid/poroid, or wrinkled for the Cantharellales and smooth or lamellate for the Clavariaceae. Hydnoid and poroid hymenophores were combined due to the very low frequency of poroid forms in the Cantharellales and the transitional hymenophore of *S. confluens*. Given the paucity of club-shaped (non-branched) taxa, these two were combined with branched forms into a single state. Sequences not identified to species were coded as typical for their genus (the most frequent state).

Ancestral State Reconstruction

Ancestral State Reconstruction (ASR) analyses were run on all traits in BayesTraits v 2 (Pagel & Meade 2014). Maximum likelihood (ML) ASR was performed on the mean height chronogram. Bayesian inference (BI) was run for 1,000,000 generations on the combined post burn-in sample of trees with

transition rate priors adjusted to reasonable values given the maximum likelihood transition rate estimates. A burn-in of 10,000 was used.

Diversification analyses

Binary State Speciation and Extinction (BiSSE: Maddison et al. 2007) was implemented in the *diversitree* package (FitzJohn 2012) in R (R Development Core Team 2013) The Akaike information criterion (AIC) was used to select the best model of evolution per dataset. Incomplete taxon sampling was implemented by summing species estimates per trait using estimates from Kirk et al. (2008). Incomplete taxon sampling estimates were doubled to assess the effect of underestimation of species diversity. BiSSE was run for five thousand generations and convergence was assessed for using effective samples size using the package coda (Plummer et al. 2006). If convergence was not achieved the analysis was run for 10,000 generations. A burn-in of 1,000 generations was used. Net diversification rate was calculated by subtracting extinction rate from speciation rate.

Multiple State Speciation and Extinction (MuSSE) (FitzJohn 2012) was implemented as above with BiSSE to test the effect of fruiting body morphology and hymenophore on diversification rate. Species were coded as resupinate, clavarioid, or pileate for the Cantharellales dataset and resupinate, clavarioid, branched, or pileate for the Clavariaceae dataset. Hymenophore was coded as smooth, hydnoid/poroid, or wrinkled for the Cantharellales dataset and smooth or lamellate for the Clavariaceae dataset.

Bayesian Analysis of Macroevolutionary Mixtures (BAMM: Rabosky 2014) was used to check for increases in diversification rate independent of character state. BAMM was run for 10 million generations with priors generated by BAMMtools (Rabosky et al. 2014). A ten percent burn-in was used and convergence was checked using coda (Plummer et al. 2006). A Bayesfactor test was used to select the best rate shift model. A 95% credible set of shift configurations was calculated from the post burn-in run. If a rate shift was detected for a specific clade in the BAMM credible set of shift configurations, BiSSE and MuSSE were rerun excluding the clade that exhibited a significant rate shift in order to test if the rate shift clade was driving any trait specific differences in diversification. Analyses were run following the methodology used above.

Results

Phylogenetic Reconstruction

The order Canatharellales was reconstructed as a monophyletic group containing the Ceratobasidiaceae, Botryobasidiaceae, Tulansellaceae, Hydnaceae, Clavulinaceae, Cantharellaceae, and a polyphyletic *Sistotrema* s.l. within the Hydnaceae, Clavulinaceae or incertae sedis (Figure 14). All families were recovered with high support except for the Clavulinaceae and Hydnaceae.

Figure 14. Absolute time-calibrated Bayesian molecular phylogenetic reconstruction of the order Cantharellales. Thickness of branches correspond to posterior probability with the doubly thickened branches indicating greater than 95% posterior probability and singly thickened branches indicating 89-95% posterior probability. Black circles along a branch indicates an increase in diversification rate within the 95% credible shift set recovered in BAMM with incomplete taxon sampling. A gray circle indicates branches with an increase in diversification rates detected at double incomplete taxon sampling estimates. A circle with a black outline indicates branches at which the single best shift configuration identified a rate increase. Dates and 95% confidence intervals for specific nodes are given in millions of years before present. Geological periods are indicated at the bottom of the phylogeny. Numbered nodes correspond to ancestral state reconstructions presented in Table 9. Character states are indicated to the right of the tips for nutritional mode, Fruiting body, and Hymenophore. The character state key is as follows; Nutritional mode: black=ECM, grey=lichenized, white=saprotrophic, half white/half grey=ECM or Saptrotrophic; Fruiting body: black=pileate, grey=branched, white=resupinate; Hymenophore: black=wrinkled, grey=hydnoid, x=poroid, white=smooth. Generic and familial classification is indicated to the right of the phylogeny. Generic abbreviation key is as follows: B.=Burgella, Ca.=Cantharellus Cb.=Ceratobasidium, Cc.=Clavulicium, Cl.=Clavulina, Cr.=Craterellus, Hd.=Hydnum, Mc.=Multiclavula, Rz.=Rhizoctonia, S.=Sistotrema, Th.=Thanatephorus, T.=Tulasnella. Inset A: Probability density of diversification rates for saprotrophic versus biotrophic nutritional modes with the Ceratobasidiaceae and Tulasnellaceae coded as saprotrophic. Inset B: Probability density of diversification rates for ECM versus non-ECM nutritional modes with the Ceratobasidiaceae and Tulasnellaceae coded as saprotrophic. Inset C: Probability density of diversification rates for saprotrophic versus biotrophic nutritional modes with the Ceratobasidiaceae and Tulasnellaceae coded as biotrophic. Inset D: Probability density of diversification rates for resupinate versus pileate and branched fruiting body morphology. Inset E: Probability density of diversification rates for smooth versus complex (wrinkled, hydnoid, and poroid) hymenophores.

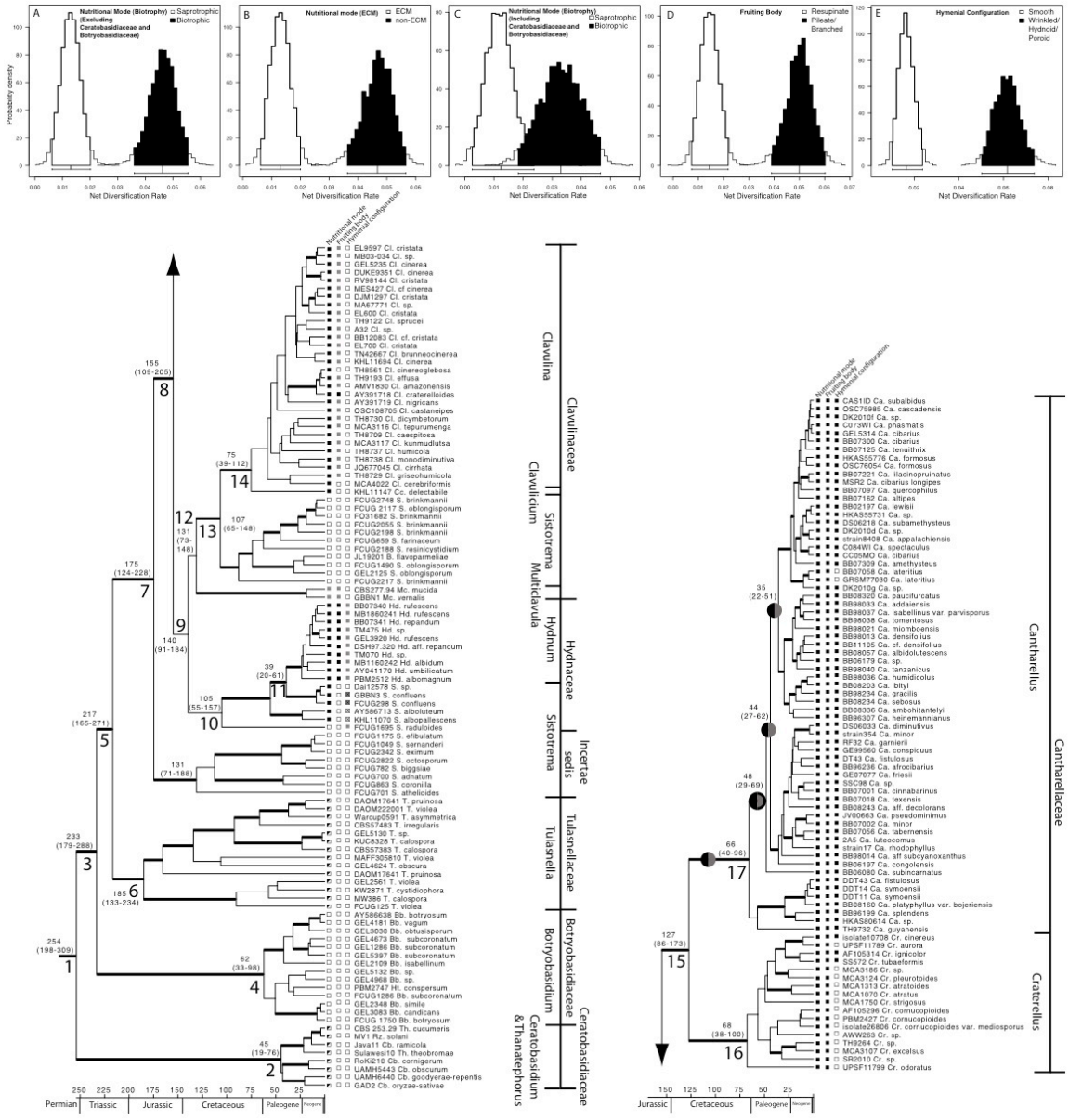

Figure 14 Continued

Relationships were found to be consistent with previous findings (Moncalvo et al. 2006) except for the strongly supported placement of the Tulasnellaceae and some members of *Sistorema* s.l. This may be due to the increased taxon and gene sampling. *Sistotrema* was found to be in two separate clades and in a paraphyletic assemblage in the family Hydnaceae. The Hydnaceae includes *Hydnum,* ECM species of *Sistotrema* (including the type species), and possibly the lignicolous hydnoid *Sistorema raduloides* although included with poor support. The family *Clavulinaceae* (*Clavulina*, *Multiclavula*, and *Sistotrema* p.p.) was the only family recovered with poor support. Biotrophy was inferred as derived in six independent lineages in the Cantharellales with one lichenized lineage (*Multiclavula*) and three ECM lineages (Cantharellaceae, *Clavulina*, and Hydnaceae) and the families Ceratobasidiaceae and Tulasnellaceae, which are considered to be typically saprotophic but also contain facultative plant parasites, become involved in orchid mycorrhizae, or occasionally ECM symbionts (Tedersoo et al. 2010). It is unknown how many ECM taxa there are or if the ECM taxa within these two families form monophyletic groups.

The Cantharellales was found to diverge from the remainder of the Agaricomycotina in the late Carboniferous through the late Triassic (211 through 321 mya, mean of 264; Figure 14). ECM lineages diverged as early as the late Jurassic (228 mya) in the Cantharellaceae to as late as the Neogene (20 mya) in the Hydnaceae. ECM lineages began diversifying later with crown node ages in the early Cretaceous (Cantharellaceae; mean=127 mya), the late Cretaceous (*Clavulina* s.l.; mean=75 mya), and the Eocene (Hydnaceae; mean=39 mya).

The Clavariaceae was reconstructed with relationships consistent with previous works (Kautmanová et al. 2013, Birkebak et al. 2013) but with the addition of the genus *Hirticlavula*, a recently described genus in the family that was recovered in a similar position as Petersen et al. (2014) (Figure 15). This genus was found to be sister to *Clavicorona-Clavaria-Camarophyllopsis* s. l. with strong support. The genus *Hyphodontiella*, however, was recovered with a different placement than previously reconstructed (Birkebak et al. 2013, Petersen 2014) with moderate support and sister to the rest of the Clavariaceae excluding *Mucronella*. This lineage has not received strong supported for placement in either previous study to include it.

Biotrophic species were recovered in two separate lineages (*Clavulinopsis* and *Ramariopsis*, and *Clavaria* and *Camarophyllopsis* s.l.). The saprotrophic genera *Mucronella*, *Hyphodontiella* and *Hirticlavula* are lignicolous while the genus *Clavicorona* is humicolous.

The Clavariaceae split from the remainder of the Agaricales in the early Jurassic through the early Cretaceous (114 through 185 mya, mean=150 mya; Figure 15). Biotrophic clades diverged as early as the early Cretaceous (138 mya) to as recent as the Paleocene (58 mya). Both biotrophic lineages began diversifying nearly contemporaneously as early as the early Cretaceous or as late as the Paleocene (mean=75 and 83 mya).

Figure 15. Absolute time-calibrated Bayesian molecular phylogenetic reconstruction of the family Clavariaceae. Thickness of branches correspond to posterior probability with the doubly thickened branches indicating greater than 95% posterior probability and singly thickened branches indicating 89-95% posterior probability. Black circles along a branch indicates a branch with an increase in diversification rate within the 95% credible shift set recovered in BAMM with incomplete taxon sampling. A gray circle indicates branches with an increase in diversification rate detected at double incomplete taxon sampling estimates. Dates and 95% confidence intervals for specific nodes are given in millions of years before present. Geological perioda are indicated at the bottom of the phylogeny. Numbered nodes correspond to ancestral state reconstructions presented in Table 9. Character states are indicated to the right of the tips for nutritional mode, Fruiting body, and Hymenophore. The character state key is as follows; Nutritional mode: black=ECM, white=saprotrophic; Fruiting body: black=pileate, grey=branched, white=club-shaped, X=resupinate; Hymenophore: black=lamellate, white=smooth. Generic and familial classification is indicated to the right of the phylogeny. Generic abbreviation key is as follows: C.=Clavaria, Cm.=Camarophyllopsis, Cu.=Clavulinopsis, Cv.=Clavicorona, H.=Hodophilus, L.=Lamelloclavaria, M.=Mucronella, R.=Ramariopsis. Inset A: Probability density of diversification rates for saprotrophic versus biotrophic nutritional modes. Inset B: Probability density of diversification rates for branched, club-shaped, and pileate fruiting body morphology. Inset C: Probability density of diversification rates for smooth versus lamellate hymenophores.

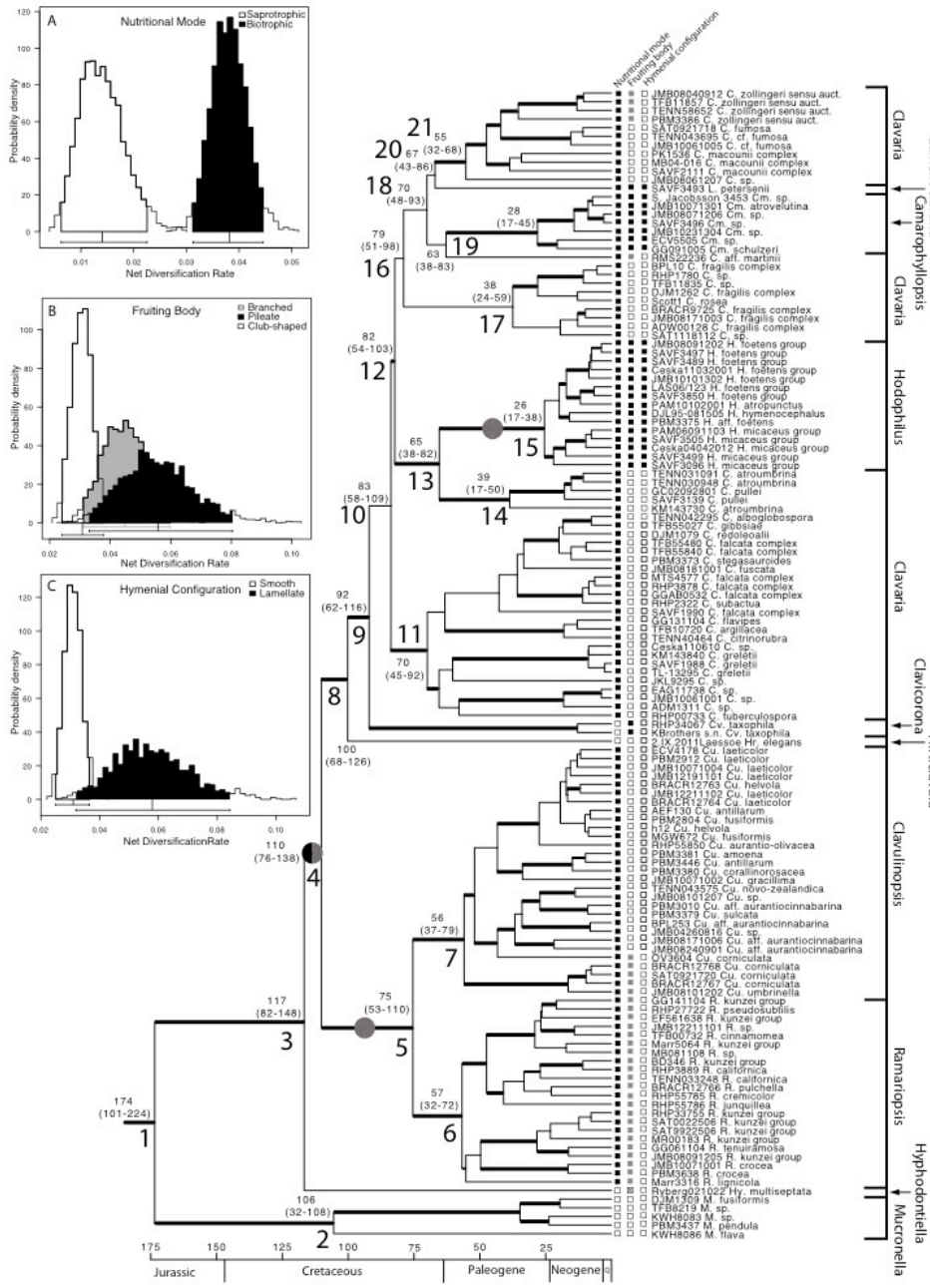

Figure 15 Continued

Ancestral State reconstruction

Both BI and ML methods reconstructed the ancestral state of nutritional mode for the Cantharellales as saprotrophic with robust support if the Ceratobasidiaceae and Tulasellaceae are coded as saprotrophic (Table 8). When they are coded as ambiguous the saprotrophic mode is only supported with ML ASR. One transition to a biotrophic nutritional mode was recovered at the node leading to the Clavulinaceae-Hydnaceae-Cantharellaceae or three separate transitions were recovered on the branch to each family with and without the Ceratobasidiaceae and Tulasnellaceae coded as saprotrophic and biotrophic respectively. The latter would infer two reversals from biotrophic to saprotrophic nutritional modes. If the Ceratobasidiaceae and Tulasnellaceae are considered saprotrophic, biotrophy is exclusively confined to nonresupinate lineages with the exception of the two ECM species *S. albopallescens* and *S. alboluteum*.

The ancestral fruiting body morphology of the Cantharellales was found to be resupinate with strong support. One robustly supported transition to nonresupinate or three robustly supported transitions (one to branched, two to pileate) were detected using BI and ML methods respectively. There was at least

Table 8. Bayesian inference and maximum likelihood ancestral state reconstruction of nutritional mode, fruiting body, and hymenophore for specific nodes of the Cantharellales phylogeny indicated on Figure 1. *=significantly supported by both Bayesian inference and maximum likelihood, **= significantly supported by Bayesian inference only, *= significantly supported by maximum likelihood only, N.S.=Not Significant.**

Node	Biotroph (Ceratobasidiaceae + Tulasnellaceae coded SAP)	Biotroph (Ceratobasidiaceae + Tulasnellaceae coded as ambig)	Fruiting Body	Hymenophore
Node 1	Saprotroph***	Saprotroph*	Resupinate***	Smooth***
Node 2	Saprotroph***	Saprotroph*	Resupinate***	Smooth***
Node 3	Saprotroph***	Saprotroph*	Resupinate***	Smooth***
Node 4	Saprotroph***	Saprotroph***	Resupinate***	Smooth***
Node 5	Saprotroph (N.S.)	Saprotroph*	Resupinate***	Smooth***
Node 6	Saprotroph***	Saprotroph*	Resupinate***	Smooth***
Node 7	Biotroph (N.S.)	Saprotroph*	Resupinate***	Smooth***
Node 8	Biotroph***	Saprotroph*	Resupinate (N.S.)	Smooth (N.S.)
Node 9	Biotroph*	Saprotroph*	Resupinate**	Hydnoid/Poroid*
Node 10	Biotroph***	Biotroph***	Pileate (N.S.)	Hydnoid/Poroid***
Node 11	Biotroph***	Biotroph***	Pileate***	Hydnoid/Poroid***
Node 12	Biotroph*	Saprotroph*	Resupinate (N.S.)	Smooth*
Node 13	Biotroph (N.S.)	Saprotroph*	Resupinate**	Smooth***
Node 14	Biotroph***	Biotroph***	Branched*	Smooth***
Node 15	Biotroph***	Biotroph***	Pileate***	Wrinkled (N.S.)
Node 16	Biotroph***	Biotroph***	Pileate***	Smooth***
Node 17	Biotroph***	Biotroph***	Pileate***	Wrinkled***

Table 9. Bayesian inference and maximum likelihood ancestral state reconstruction of nutritional mode, fruiting body, and hymenophore for specific nodes of the Cantharellales phylogeny indicated on Figure 1. *=significantly supported by both Bayesian inference and maximum likelihood, N.S.=Not Significant.**

Node	Nutritional mode	Fruiting body	Hymenophore
Node1	Saprotroph***	Club-shaped***	Smooth***
Node 2	Saprotroph***	Club-shaped***	Smooth***
Node 3	Saprotroph***	Club-shaped***	Smooth***
Node 4	Saprotroph***	Club-shaped***	Smooth***
Node 5	Biotroph***	Club-shaped***	Smooth***
Node 6	Biotroph***	Branched (N.S.)	Smooth***
Node 7	Biotroph***	Club-shaped***	Smooth***
Node 8	Saprotroph***	Club-shaped***	Smooth***
Node 9	Saprotroph***	Club-shaped***	Smooth***
Node 10	Biotroph***	Club-shaped***	Smooth***
Node 11	Biotroph***	Club-shaped***	Smooth***
Node 12	Biotroph***	Club-shaped***	Smooth***
Node 13	Biotroph***	Club-shaped***	Smooth***
Node 14	Biotroph***	Club-shaped***	Smooth***
Node 15	Biotroph***	Pileate (N.S.)	Lamellate***
Node 16	Biotroph***	Club-shaped***	Smooth***
Node 17	Biotroph***	Club-shaped***	Smooth***
Node 18	Biotroph***	Club-shaped***	Smooth***
Node 19	Biotroph***	Pileate (N.S.)	Lamellate***
Node 20	Biotroph***	Club-shaped***	Smooth***
Node 21	Biotroph***	Club-shaped***	Smooth***

one transition from branched to pileate fruiting bodies in the Clavulinaceae (*Clavulina craterelloides*).

Hymenophore was inferred as smooth with strong support regardless of ASR methodology in the Cantharellales. Both methods robustly infer a single transition to hydnoid/poroid and one to three transitions to a wrinkled hymenophore. Two reversals to a smooth hymenophore are detected but only one receives strong support (*Cantharellus lateritius*).

The ancestral nutritional mode of the Clavariaceae was found to be saprotrophic and was reconstructed as such along the backbone of the phylogenetic reconstruction with robust support (Table 9). Two strongly supported transitions to biotrophy were detected: one leading to the *Ramariopsis-Clavulinopsis* clade and the other leading to the *Clavaria-Camarophyllopsis-Hodophilus* clade. No reversals were detected.

Ancestral state reconstruction of fruiting body morphology of the family was recovered as club shaped and on the entire backbone of the tree. Four independent transitions to both branched lineages and pileate lineages were detected while one transition to resupinate fruiting bodies was found. There was no strong support for any reversal back to a club-shaped fruiting body.

A smooth hymenophore was found to be the ancestral state of the Clavariaceae and along the backbone with three independent transitions to lamellate lineages leading to the three agaricoid lineages.

Diversification analyses

BAMM detected a credible set of rate shifts along the branch leading to the genus *Cantharellus* (Figure 14, node 17; wrinkled hymenophore and ECM nutritional mode) or on the next three subsequent branches within the genus. The first and second crown groups within the genus *Cantharellus* make up the vast majority of the credible shift set of the rate shifts (80% with incomplete taxon sampling, 90% with double the estimates of incomplete taxon sampling). The branches with rate shifts in the credible shift set did not vary with respect to the degree of incomplete taxon sampling. The single best shift configuration indicated a shift at the first crown group within the Cantharellales regardless of the degree of incomplete taxon sampling (Figure 14).

BAMM detected a single rate shift in the Clavariaceae with incomplete taxon sampling on a branch leading to a node not associated with any specific trait shift though it does exclude the two earliest diverging saprotrophic lineages (Figure 14, node 4). When incomplete taxon sampling is doubled, to account for unknown diversity, two more rate shifts are detected in addition to the previous shift: the first on the branch leading to the *Ramariopsis-Clavulinopsis* clade (Figure 15, node 5) and a second on the branch leading to the genus *Hodophilus* (Figure 15, node 15).

Lineages with biotrophic and ECM nutritional modes were shown to have higher diversification rates than saprotrophic lineages in the Cantharellales (Figure 14A & B) regardless of the degree of incomplete taxon sampling as long as the families Ceratobasidiaceae and Tulasnellaceae were coded as saprotrophic. The diversification rate estimates of ECM and biotrophy were not significantly different and were, in fact, nearly identical. Neither trait was shown to exhibit a significantly increased diversification rate when the Certobasidiaceae and Tulasnellaceae were coded as biotrophic or ECM (Figure 14C; ECM not shown).

A model with combined diversification parameters for branch-clavarioid and pileate lineage was a substantially better fit than a model with each nonresupinate state coded separately in BiSSE. Nonresupinate lineages had significantly higher diversification rates than resupinate lineages regardless of degree of incomplete taxon sampling (Figure 14D).

The best-fit model for hymenophore was found to be one in which complex hymenophores (wrinkled, hydnoid and poroid) were combined. These complex hymenophores were associated with significantly faster diversification rates than lineages with smooth hymenophores (Figure 14E).

In order to insure that the genus *Cantharellus*, which was found to have an increased diversification rate with trait independent BAMM analyses, was not driving the pattern of increased diversification for biotrophy and fruiting body, BiSSE analyses were rerun excluding the genus *Cantharellus*. This could not be done with hymenophores, as it would have excluded to great a proportion of the species with complex hymenophores. A highly biased trait ratio has been shown to affect BiSSE's performance (Davis et al. 2013). None of these additional

analyses significantly deviated from the results that included the genus *Cantharellus*.

The nutritional mode of the family Clavariaceae was found to significantly influence the net diversification rate. Biotrophic lineages had a higher diversification rate than saprotrophic lineages regardless of the degree of incomplete taxon sampling (Figure 15A). When the two clades associated with increased diversification rate identified in BAMM were excluded and subsequently analyzed in BiSSE the diversification rate of the biotrophic lineages was found to be slower but not significantly so (data not shown).

Though pileate lineages were found to have the highest diversification rate, this was not significantly faster in lineages with different fruiting body morphologies. Branched fruiting bodies were found to diversify at a rate intermediate between club-shaped and pileate groups but the difference was not significant (Figure 15B). Reanalysis excluding quickly evolving lineages detected in BAMM were not conducted because the resulting frequency of states are then too low for pileate and branched lineages.

Lamellate lineages in the family in the Clavariaceae were found to diversify faster, although not significantly (Figure 15C). The difference, however, did become significant when incomplete taxon sampling was doubled. Exclusion of lamellate lineages would result in too small a frequency of lamellate lineages to analyze with BiSSE based on the limitations of SSE models.

Discussion

Transitions in nutritional mode

Both the Cantharellales and Clavariaceae were found to have increased diversification rates associated with a biotrophic nutritional mode. This result was not supported when the Ceratobasidiaceae and Tulasnellaceae in the Cantharellales are entirely considered biotrophic. However, this latter scenario is not realistic because only a few species in each lineage are known to form ectomycorrhizae. Unfortunately, there is currently no way to include ambiguous character states in BiSSE analyses. The Cantharellales showed an approximate 3-fold increase in diversification rate while the Clavaraiaceae exhibited an approximate 2.5-fold increase. These results were not affected by incomplete taxon sampling or the removal of clades found to have a significantly increased diversification rate. It is important to note, however, that in these clades biotrophy is highly correlated with more complex (branched and pileate) lineages. This is the first study to support the hypothesis that evolution of biotrophic interactions in the Basidiomycota is associated with an increase in overall diversification rates.

Biotrophy did not evolve contemporaneously in all lineages, although most began diversifying in the Cretaceous. These dates are consistent with recent studies on the Tuberaceae (Bonito et al. 2012) and Inocybeaceae (Matheny et al. 2009). These authors associate the divergence and diversification of these ECM lineages with the early radiation of Angiosperms. Such claims may need to be

reevaluated as no known ECM host plant lineages had yet evolved. The oldest Angiosperm ECM lineage is the Fagales, which did not diverge until nearly 100 mya (Bell et al. 2010), thus suggesting that the ancestors of these groups as well as the Cantharellales must have associated with Pinaceae. Ancestral plant associations in the Clavariaceae are not known, but it seems both lineages could have diversified with angiosperms in the late Cretaceous.

Transitions in fruiting body morphology

Lineages that produce more complex fruiting bodies (pileate and branched) diversified 3-times faster than resupinate lineages in the Cantharellales. No strong differences were found between diversification rates of lineages with different fruiting bodies in the Clavariaceae. Merely comparing fruiting body structure may not be a fair comparison because some simple club-shaped species produce abundant clusters of individual clubs while branched species may be sparsely branched. A quantitative comparison of overall spore production area may provide a more informative character. As mentioned above, complex fruiting bodies could be promoting diversification in the Agaricomycetes, but this trait is highly correlated with biotrophy in these lineages.

The ancestral state of the Cantharellales was found to be resupinate from which one or two transitions to branched or club-shaped lineages (*Clavulina* and *Multiclavula*) and two transitions to pileate lineages (*Hydnum* and Cantharellaceae) occured. Within the genus *Clavulina* two reversals to resupinate fruiting bodies, as well as one transition to pileate forms occured supporting the idea that clavarioid fruiting bodies are a highly labile morphology (Hibbett 2004) and that they constitute an important transitional state in fruiting body evolution (Birkebak et al. in review).

The most recent common ancestor of the Clavaraiceae was inferred as a club-shaped followed by four transitions to both branched fruiting bodies and pileate lineages and one transition to a resupinate all between the late Cretaceous and late Paleogene. This differs from the previous study (Birkebak et al. in review) that was not able to strongly support four independent transitions to pileate fruting bodies from club-shaped ancestors. These findings in the Clavariaceae provide further support for the clavarioid fruiting body as a labile and important transitional state that gives rise to numerous other morphologies.

Transitions in hymenophore

Complex hymenophores were found to increase diversification rate nearly 3.5-fold in the Cantharellales. Wrinkled and hydnoid/poroid hymenophores did not significantly differ in diversification rate. The results presented here support the findings of Birkebak et al. (in review) that lamellate lineages are not diversifying significantly faster than more simple hymenophores. Note that in this dataset lamellate hymenophore and pileate fruiting bodies are completely correlated with the exception of *Clavicorona*. As mentioned above, a quantitative calculation of

hyemnial surface area may be a more informative character to test for associated changes in diversification rate.

One or two transitions to a hydnoid hymenophore were detected in the Hydnaceae. Two species have a poroid hymenophore while the species *Sistotrema confluens* has an hymenophore that is intermediate between poroid and hydnoid depending on age of development. Most species of *Craterellus* have a smooth hymenium while and one or two transitions to a wrinkled hymenium. The entire genus *Cantharellus* has a wrinkled hymenium with the exception of *Cantharellus lateritius*, which represents a reversal back to a smooth hymenium.

A smooth hymenophore is strongly support as the ancestral state for the Clavariaceae with three independent transitions to a lamellate state. This differs from previous investigation (Birkebak et al. in review) in that they were not able to robustly support three independent transitions as are supported here.

Conclusions

With respect to the family Clavariaceae and the order Cantharellales support was found for the hypothesis that biotrophy (including transitions to an ECM state) is associated with increased diversification rates. Lineages with complex hymenophores in the order Cantharellales are also associated with increased diversification rates. It is currently unclear, however, which trait may be driving this trend as biotrophic lineages in the Cantharellales are also typically pileate or branched, although no increase in diversification associated with fruiting body morphology was detected in the Clavariaceae. Similarly, hymenophores that increase spore production area were found to be associated with an increase in diversification rate only in the Cantharellales but not in the Clavariaceae. This may be the character driving the increased diversification rate shift in the genus *Cantharellus*.

Investigations into the patterns and drivers of diversification in other lineages in the Agaricomycetes are needed in order to uncover whether the associations found here are generalizable across the class. The orders Gomphales and Thelephorales are both comprised of a diverse assemblage of morphological and ecological diversity and would be ideal additional lineages to test for such diversification rate changes. These groups were preliminarily investigated but, unfortunately, there is not sufficient sampling publically availed at this time to reconstruct well supported and sampled phylogenies (data not shown). Additional traits should also be explored to test alternative explanations for patterns uncovered using diversification rate analyses.

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Appendix

Table 10. Sequences used in the Cantharellales phylogenetic reconstruction with associated GenBank numbers.

Taxon	Collection Number	LSU	rpb2	tef-1
Dacrymyces sp.	FPL 8953	AY691892	DQ381845	DQ028587
Pyrenogaster pityophilus	OSC59743	DQ218519	DQ219057	DQ219232
Ceratorhiza oryzae-sativae	GAD2	JQ920471		
Ceratobasidium goodyerae-repentis	UAMH 6440	AY243523		
Ceratobasidium obscurum	UAMH 5443	AY243526		
Ceratobasidium cornigerum	UAMH 5443	AY243526		
Ceratobasidium ramicola	Java11	HQ424243		
Thanatephorus theobromae	Sulawesi-10	HQ424242		
Rhizoctonia solani	MV-1	JX576188		
Thanatephorus cucumeris	CBS 253.29	DQ917658		
Botryobasidium botryosum	FCUG 1750	DQ089013		
Botryobasidium candicans	GEL3083	AJ406440		
Botryobasidium simile	GEL2348	DQ898730	DQ898770	
Botryobasidium subcoronatum	FCUG1286	AY647212	DQ366284	
Haplotrichum conspersum	PBM 2747	DQ521414		DQ52142
Botryobasidium sp.	GEL4968	AJ406444		
Botryobasidium sp.	GEL5132	AJ406445		
Botryobasidium isabellinum	GEL2109	AF393047	AY218475	
Botryobasidium subcoronatum	GEL5397	AJ406443		
Botryobasidium subcoronatum	GEL1286	AF393048		
Botryobasidium subcoronatum	GEL4673	AJ406442		
Botryobasidium obtusisporum	GEL3030	DQ898729	DQ898769	
Botryobasidium vagum	GEL4181	AJ406439		
Botryobasidium botryosum	KHL11081	AY586638		
Tulasnella violea	FCUG125		DQ381841	
Tulasnella calospora	MW 386	AY152407		
Tulasnella cystidiophora	KW2871	AY585831		
Tulasnella violea	GEL2561		DQ898768	
Tulasnella pruinosa	DAOM 17641	AY293216	DQ381839	DQ061274
Tulasnella obscura	GEL4624	AJ406435		
Tulasnella violea	MAFF305810		DQ521418	
Tulasnella calospora	CBS 573.83	AY243521		
Tulasnella calospora	KUC8328	FJ471579		
Tulasnella sp.	GEL5130	DQ898731	DQ898771	

Table 10 Continued

Taxon	Collection Number	LSU	rpb2	tef-1
Tulasnella irregularis	CBS 574.83	AY243519		
Tulasnella asymmetrica	Warcup 0591	AY152406		
Tulasnella violea	DAOM 222001	AY293216		
Sistotrema athelioides	FCUG701	DQ898700	DQ898766	
Sistotrema coronilla	FCUG863	DQ457641		
Sistotrema adnatum	FCUG700	DQ898699	DQ898763	
Sistotrema biggsiae	FCUG782	DQ898697		
Sistotrema octosporum	FCUG2822	DQ898698	DQ898764	
Sistotrema eximum	FCUG2342	DQ898695	DQ898762	
Sistotrema sernanderi	FCUG1049	AY647215		
Sistotrema efibulatum	FCUG1175	DQ898696		
Sistotrema raduloides	FCUG1695	DQ898710	DQ898765	
Sistotrema albopallescens	KHL11070	AM259210		
Sistotrema alboluteum	TAA167982	AY586713		
Sistotrema confluens	FCUG298	AY647214	DQ381837	
Sistotrema confluens	Dai12578	JX076811		
Hydnum albomagnum	PBM2512	AY700199	DQ234553	DQ234568
Hydnum umbilicatum		AY041170		
Hydnum albidum	MB1160242	AY293186		
Hydnum sp.	TM070	DQ898744	DQ898750	
Hydnum aff. repandum	DSH97.320		DQ366288	
Hydnum rufescens	GEL3920	AJ406427		
Hydnum sp.	TM475	DQ898743	DQ898751	
Hydnum repandum	BB 07.341	KF294643	KF294720	JX192980
Hydnum rufescens	MB18-6024/1	AY293187		
Hydnum rufescens	BB 07.340	KM484698		
Multiclavula vernalis	GB-BN-1	AM259214		
Multiclavula mucida	CBS277.94	AY885163		
Sistotrema brinkmannii	FCUG2217	DQ898709	DQ898755	
Sistotrema oblongisporum	GEL2125	DQ898728	DQ898767	
Sistotrema oblongisporum	FCUG1490	DQ898702	DQ898758	
Burgella flavoparmeliae	JL192-01	DQ915469		
Sistotrema resinicystidium	FCUG2188	DQ898708	DQ898760	
Sistotrema farinaceum	FCUG659	DQ898707	DQ898756	
Sistotrema brinkmannii	FCUG2198	DQ898705	DQ898753	
Sistotrema brinkmannii	FCUG2055	DQ898706	DQ898754	

Table 10 Continued

Taxon	Collection Number	LSU	rpb2	tef-1
Sistotrema brinkmannii	FO31682	AJ406431		
Sistotrema oblongisporum	FCUG2117	DQ898703	DQ898759	
Sistotrema brinkmannii	FCUG2748	DQ898704	DQ898752	
Clavulicium delectabile	KHL11147	AY586688		
Clavulina cerebriformis	MCA4022	JN228222	JN228233	
Clavulina griseohumicola	TH8729	DQ056366		
Clavulina cirrhata	MCA3184	JQ677045		
Clavulina monodiminutiva	TH8738	DQ056372	JN228237	
Clavulina humicola	TH8737	DQ056367	JN228244	
Clavulina kunmudlutsa	MCA3117	HQ680362		
Clavulina caespitosa	TH8709	DQ056370	JN228234	
Clavulina tepurumenga	MCA3116	HQ680363	JN228248	
Clavulina dicymbetorum	TH8730	DQ056369		
Clavulina castaneipes	OSC108705	EU669261		
Clavulina nigricans		AY391719		
Clavulina craterelloides		AY391718		
Clavulina amazonensis	AMV1830	KF714513		
Clavulina effusa	TH9193	JN228230	JN228245	
Clavulina cinereoglebosa	TH8561	JN228232	JN228246	
Clavulina cinerea	KHL11694	EU118616		
Clavulina brunneocinerea	TN42667	JN228220		
Clavulina cristata	EL700	AM259213		
Clavulina cf. cristata	BB 12.083	KM484694		
Clavulina sp.	A32	AJ534893		
Clavulina sprucei	TH9122	JN228223	JN228236	
Clavulina cristata	EL600	AM259212		
Clavulina sp.	MA67771	JQ415957		
Clavulina cristata	DJM1297	DQ284901		
Clavulina cf. cristata	MES427	JN228225		
Clavulina cristata	RV98/144	AF261553		
Clavulina cinerea	DUKE9351	JN228216	JN228251	
Clavulina cinerea	GEL5235	AJ406433		
Clavulina sp.	MB03-034	AY745694	DQ366286	DQ028589
Clavulina cristata	EL95_97	AY586648		
Craterellus odoratus	UPSF11799	AF105306		
Craterellus sp.	MSR8	HQ450771		

Table 10 Continued

Taxon	Collection Number	LSU	rpb2	tef-1
Craterellus excelsus	MCA3107	JQ91512		
Craterellus sp.	TH9264	JQ915138		
Craterellus sp.	AWW263	JQ915117		
Craterellus corncopioides var. mediosporus	Isolate268-06	JF412275		
Craterellus cornucopioides	PBM2427	AY700188	DQ366287	
Craterellus cornucopioides		AF105296		
Craterellus strigosus	MCA1750	JQ915120		
Craterellus atratus	MCA1070	JQ915118		
Craterellus atratoides	MCA1313	JQ915119		
Craterellus pleurotoides	MCA3124	JQ915123		
Craterellus sp.	MCA3186	JQ915124		
Craterelllus tubaeformis	SS572	JQ976980		
Craterellus ignicolor		AF105314		
Craterellus aurora	UPSF11789	AF105302		
Craterellus cinereus	Isolate107-08	JF412276		
Cantharellus guyanensis	TH9732	KC897656		
Cantharellus hygrophorus	HKAS80614	KJ004002		KJ004003
Cantharellus splendens	BB 96.199	KF294671	KF294749	
Cantharellus platyphyllus subsp. Bojeriensis	BB 08.160	KF294648	KF294725	X192984
Cantharellus symoensii	DDT11	JQ976953		
Cantharellus symoensii	DDT43	JQ976965		
Cantharellus subincarnatus	BB06.080	KF294601	KF294675	
Cantharellus aff. congolensis	BB06.197	KF294608	KF294683	GQ914982
Cantharellus aff. subcyanoxanthus	BB 98.014	KF294615.	KF294689	JX192973
Cantharellus rhodophyllus	strain17	HM750925		
Cantharellus luteocomus	2A5	AB973796		
Cantharellus taberensis	BB07.056	KF294631	KF294706	
Cantharellus minor	BB07.002	KF294625	KF294699	JX192978
Cantharellus pseudominimus	JV 00.663	KF294657	KF294735	JX192991
Cantharellus aff. decolorans	BB08.243	KF294653	KF294730	JX192987
Cantharellus texensis	BB07.018	KF294626	KF294701	
Cantharellus cinnabarinus	BB07.001	KF294624	KF294698	
Cantharellus sp.	SSC98	KF801100		KF801095
Cantharellus friesii	GE07.077	KF294659	KF294737	
Cantharellus afrocibarius	BB96.236	KF294669	KF294747	JX192994
Cantharellus fistulosus	DDT43	KF294674		JX192997

Table 10 Continued

Taxon	Collection Number	LSU	rpb2	tef-1
Cantharellus conspicuus	GE99.560		KF294751	
Cantharellus gernierii	RF32	AY392767		
Cantharellus minor	strain354	HM750923		
Cantharellus dimenutivus	DS06.033	KF294661	KF294740	
Cantharellus heinemannianus	BB96.307	KF294665	KF294743	
Cantharellus ambohitantelyi	BB08.336	KF294656	KF294733	JX192989
Cantharellus sebosus	BB08.234	KF294652	KF294729	JX192986
Cantharellus gracilis	BB98.234	KF294612	KF294686	JX192970
Cantharellus ibityi	BB08.203	KF294651	KF294728	JX192985
Cantharellus humidicolus	BB98.036	KF294666	KF294744	JX193005
Cantharellus tanzanicus	BB98.040	KF294622	KF294696	JX192977
Cantharellus sp.	BB06.179	KF294607	KF294681	JX192968
Cantharellus albidolutescens	BB08.057	KF294645	KF294722	KF294752
Cantharellus sp.	BB06.179	KF294607	KF294681	JX192968
Cantharellus miomboensis	BB98.021	KF294613	KF294687	JX192971
Cantharellus tomentosus	BB98.038	KF294610	KF294684	GQ914965
Cantharellus isabellinus var. parvisporus	BB98.037	KF294611	KF294685	GQ914966
Cantharellus addaiensis	BB98.033	KF294667	KF294745	JX192992
Cantharellus paucifurcatus	BB08.320	KF294655	KF294732	JX192988
Cantharellus sp.	DK2010g	HM750930		
Cantharellus lateritius	GRSM77030	DQ898694	DQ898746	
Cantharellus lateritius	BB07.058	KF294633	KF294708	GQ914959
Cantharellus amethysteus	BB07.309	KF294642	KF294719	GQ914954
Cantharellus cibarius	CC05MO	JX030420		
Cantharellus spectaculus	CO84WI	JX030423		
Cantharellus appalachiensis	strain8408	HM750916		
Cantharellus sp.	DK2010d	HM750921		
Cantharellus subamethysteus	DS06.218	KF294664	KF294742	
Cantharellus sp.	HKAS55731	HM594682		
Cantharellus lewisii	BB02.197	KF294623	KF294697	
Cantharellus altipes	BB07.162	KF294636	KF294713	
Cantharellus quercophilus	BB07.097	KF294644	KF294721	JX192981
Cantharellus cibarius var. longipes	MSR2	HM750924		
Cantharellus lilacinopruinatus	BB07.221	KF294637	KF294714	GQ914951
Cantharellus formosus	OSC76054	AY041165		
Cantharellus formosus	HKAS55776	JF906720		

Table 10 Continued

Taxon	Collection Number	LSU	rpb2	tef-1
Cantharellus tenuithrix	BB07.125		KF294712	
Cantharellus cibarius	BB07.300	KF294641	KF294718.	GQ914950
Cantharellus cibarius	GEL5314	AJ406428		
Cantharellus phasmatis	C073WI	JX030426		
Cantharellus sp.	DK2010f	HM750926		
Cantharellus cascadensis	OSC75985	AY041163		
Cantharellus subalbidus	CAS1ID	JX030439		

Table 11. Sequences used in the Clavariaceae phylogenetic reconstruction with associated GenBank numbers.*

Taxon	Collection number	LSU	SSU	rpb2
Hygrophoropsis aurantiaca	MB03-127	AY684156	AY662663	AY786059
Hygrophorus pudorinus	PBM2721	DQ457678	DQ444861	DQ472725
Mucronella flava	KWH8086	X		X
Mucronella pendula	PBM3437	HQ829921		X
Mucronella sp.	KWH8083	X	X	
Mucronella sp.	TFB8219	X	X	
Mucronella fusiformis	DJM1309	DQ284905		
Hyphodontiella multiseptata	Ryberg021022	EU118634		
Ramariopsis lignicola	Marr3316	X		
Ramariopsis crocea	PBM3638	X	X	
Ramariopsis crocea	JMB10071001	HQ877715	X	X
Ramariopsis kunzei group	JMB08091205	X		X
Ramariopsis tenuiramosa	GG061104	EF535269		
Ramariopsis kunzei group	MR00183	HQ877720		X
Ramariopsis kunzei group	SAT9922506	X		
Ramariopsis kunzei group	SAT0022506			X
Ramariopsis kunzei group	RHP33755	X		
Ramariopsis junquillea	RHP55786	HQ877718		
Ramariopsis cremicolor	RHP55785	HQ877714		
Ramariopsis pulchella	BRACR12766	GU299496		
Ramariopsis californica	TENN033248	X		
Ramariopsis californica	RHP3889	X		
Ramariopsis kunzei	BD346	DQ284902		
Ramariopsis sp.	MB081108	X	X	
Ramariopsis aff. kunzei	Marr5064	HQ877719	X	

Table 11 Continued

Taxon	Collection number	LSU	SSU	rpb2
Ramariopsis cinnamomea	TFB00732	X		
Ramariopsis sp.	JMB12211101	X	X	
Ramariopsis kunzei	GG141104	EF561638		
Ramariopsis pseudosubtilis	RHP27722	HQ877723	X	
Ramariopsis kunzei	GG141101	EF561638	GU187647	GU187807
Clavulinopsis umbrinella	JMB08101202	X		X
Clavulinopsis corniculata	BRACR12767	GU299494		
Clavulinopsis corniculata	SAT0921720	X	X	X
Clavulinopsis corniculata	BRACR12768	GU299495		
Clavulinopsis corniculata	OV3604	X		
Clavulinopsis aff. aurantiocinnabarina	JMB08240901	HQ877703	X	X
Clavulinopsis aff. aurantiocinnabarina	JMB08171006	HQ877705	X	X
Clavulinopsis sp.	JMB04260816	X		
Clavulinopsis aff. aurantiocinnabarina	BPL253	X		X
Clavulinopsis sulcata	PBM3379	HQ877709		X
Clavulinopsis aff. aurantiocinnabarina	PBM3010	HQ877706	X	X
Clavulinopsis sp.	JMB08101207	X		X
Clavulinopsis novo-zealandica	NEED	X		
Clavulinopsis gracillima	JMB10071002	HQ877708	X	X
Clavulinopsis corallinorosacea	PBM3380	HQ877707	X	X
Clavulinopsis antillarum	PBM3446	PBM3446		X
Clavulinopsis amoena	PBM3381	HQ877702	X	X
Ramariopsis aurantio-olivacea	RHP55850	HQ877711		
Clavulinopsis fusiformis	MGW672	HQ877717	X	X
Clavulinopsis helvola	h12			LN714638
Clavulinopsis fusiformis	PBM2804	EF535273		
Clavulinopsis antillarum	AEF130	X		
Clavulinopsis laeticolor	BRACR12764	GU299509		
Clavulinopsis laeticolor	JMB12211102	X	X	
Clavulinopsis helvola	BRACR12763	GU299510		
Clavulinopsis laeticolor	JMB12191101	X	X	
Clavulinopsis laeticolor	JMB10071004	X		
Clavulinopsis laeticolor	PBM2912	X		
Clavulinopsis laeticolor	ECV4178	X		
Hirticlavula elegans	2.IX.2011 L ss e	KJ939349		
Clavaria asperulispora	K(M)143814	JN315790		
Clavicorona taxophila	KBrothers s.n.	KP257146	X	X

Table 11 Continued

Taxon	Collection number	LSU	SSU	rpb2
Clavicorona taxophila	DH003833	KP257147		
Clavaria tuberculospora	RHP00733	X		
Clavaria sp.	ADM1311	HQ877685	X	X
Clavaria sp.	JMB10061001 (TENN065665)	HQ877684		KP257260
Clavaria sp.	EAG11738	X		
Clavaria sp.	JKL9295	X		
Clavaria greletii	TL-13295	JN416778		
Clavaria greletii	SAV F1988 (SAV)	GU299504		
Clavaria greletii	K(M)143840	GU299503		
Clavaria sp	Ceska110410 (UBC)	KP257207		X
Clavaria citrinorubra	TENN040464	HQ877686		
Clavaria argillacea	TFB10710 (TENN058796)	HQ877683		
Clavaria flavipes	GG131104 (TENN063740)	EF535267		
Clavaria falcata complex	SAV F1990 (SAV)	GU299506		
Clavaria subacuta	RHP2322 (TENN048438)	HQ877699		
Clavaria falcata complex	GG_AB05-32	EF535278		
Clavaria falcata complex	RHP3878 (TENN033742)	KP257192		
Clavaria falcata complex	MTS4577 (WTU)	HQ877679	X	X
Clavaria fuscata	JMB08181001 (TENN)	HQ877691	X	KP257253
Clavaria stegasauroides	PBM3373 (TENN)	HQ877698		KP257261
Clavaria falcata complex	TFB55840 (TENN043602)	HQ877681		
Clavaria falcata complex	TFB55480	X		X
Clavaria redoleoalii	DJM1079 (MINN)	DQ284906		
Clavaria gibbsiae	TFB55027 (TENN043551)	KP257200		
Clavaria alboglobospora	TENN042295 (TENN)	HQ877682		
Clavaria atroumbrina	K(M)143730	JN315792		
Clavaria pullei	SAV F3139 (SAV)	KP257203		KP257255
Clavaria pullei	GC02092801	JN315797		
Clavaria atroumbrina	TENN030948	JN315789		
Clavaria atroumbrina	TENN031091	JN315788		
Hodophilus micaceus group	SAV F3096 (SAV)	KP257225		
Hodophilus micaceus group	SAV F-3499 (SAV)	KP257226		
Hodophilus micaceus group	Ceska040412 (UBC)	KP257219		KP257269
Hodophilus micaceus group	SAV F3505 (SAV)	KP257227		KP257271
Hodophilus micaceus group	PAM06091103 (LIP, split at TENN)	KP257224		
Hodophilus aff. foetens	PBM3375 (TENN)	KP257243		KP257284
Hodophilus hymenocephalus	DJL95-081505 (TENN)	DQ457679	X	DQ472726

Table 11 Continued

Taxon	Collection number	LSU	SSU	rpb2
Hodophilus atropuncta	PAM10102001 (LIP, split at TENN)	KP257217		KP257267
Hodophilus foetens group	SAV F3850 (SAV)	KP257241		KP257282
Hodophilus foetens group	LAS06/123 (GB0060378)	KP257242		KP257283
Hodophilus foetens group	JMB10101302 (TENN)	KP257233		KP257277
Hodophilus foetens group	Ceska110301 (UBC)	KP257228		KP257272
Hodophilus foetens group	SAV F3489 (SAV)	KP257236		
Hodophilus foetens group	SAV F3497 (SAV)	KP257238		
Hodophilus foetens group	JMB08091202 (TENN067461)	KP257235		KP257279
Clavaria sp.	SAT1118112			X
Clavaria fragilis complex	ADW0128 (TENN064092)	HQ877687		
Clavaria fragilis complex	JMB08171003 (TENN)	HQ877689	X	KP257252
Clavaria fragilis complex	BRACR9725 (BRA)	GU299499		
Clavaria rosea	Scott1 (TENN063100)	KP257205	X	KP257256
Clavaria fragilis complex	DJM1262 (MINN)	DQ287907		
Clavaria sp.	TFB11835 (TENN060720)	KP257208	X	KP257258
Clavaria sp.	RHP1780	X		X
Clavaria fragilis complex	BPL10 (TENN)	KP257197	X	KP257251
Clavaria aff. martinii	RMS22236	X		
Camarophyllopsis schulzeri	GG091005 (TENN)	EF537888	X	GU187819
Camarophyllopsis sp.	ECV5505 (TENN067613)	KP257180		
Camarophyllopsis sp.	JMB10231304	X		
Camarophyllopsis sp.	SAV F3496 (SAV)	KP257186		
Camarophyllopsis sp.	JMB08071206 (TENN067423)	KP257184		KP257249
Camarophyllopsis atrovelutina	JMB10071301 (TENN)	KP257173		KP257246
Camarophyllopsis sp.	S. Jacobsson 3453 (H)	AM946415		
Lamelloclavaria petersenii	SAV F3493 (SAV)	KP257244		KP257285
Clavaria sp	JMB08061207 (TENN)	KP257209		KP257259
Clavaria macounii complex	SAV F2111 (SAV)	GU299508		
Clavaria macounii complex	PK1536 (UBC F13537)	KP257202	X	KP257254
Clavaria macounii complex	MB04-016 (CUW)	DQ202267	DQ437680	DQ385880
Clavaria cf fumosa	JMB10061005 (TENN065659)	HQ877690		
Clavaria cf fumosa	TENN043695 (TENN)	HQ877697		
Clavaria fumosa	SAT0921718 (TENN064091)	HQ877695		X
Clavaria aff. zollingeri sensu auct.	PBM3386 (TENN)	KP257212	X	KP257264
Clavaria zollingeri sensu auct.	TENN58652	AY639882		
Clavaria zollingeri sensu auct.	TFB11857 (TENN060741)	KP257211		

Table 11 Continued

Taxon	Collection number	LSU	SSU	rpb2
Clavaria zollingeri sensu auct.	JMB08040912 (TENN064095)	HQ877700	X	KP257263

CONCLUSION

Molecular phylogenetic investigation was found to be invaluable in elucidating patterns of diversity and addressing hypotheses otherwise left to the realm of speculation and argumentation. Systematic relationships can now be objectively tested with the use of molecular sequence data aiding the refinement of taxonomic classification systems to reflect shared evolutionary history. Possible drivers of patterns of diversity in Fungi can be explored with more objective precision.

In chapter one it can be seen that revised taxonomic arrangements were uncovered for the family Clavariaceae not reflecting any existing classification schemes. Previously suggested synapomorphic traits for familial and generic definition required revision. The inferred biotrophic mode for many members of the family was a surprising result and highlights the lack of knowledge concerning basic lifestyle traits of some fungal lineages.

Equally poorly understood are the patterns of fruiting body morphology and their effect on diversification rates, further explored in chapter two. Despite the disparity in diversity of different morphologies, no empirical testing of hypotheses concerning effects of morphological traits on diversification rate had previously been performed. Partial support was found for the Corner hypothesis of fruiting body evolution in the family Clavariaceae. Despite the detection of multiple shifts to more complex fruiting bodies and increases in spore production area, no significant correlation between pileate or lamellate lineages and higher diversification rates were detected compare to related clavarioid lineages.

An additional order, the Cantharellales, and an expanded dataset of the family Clavariaceae were created to further explore the effects of ecology and morphology on diversification rate in the third chapter of this dissertation. Support that biotrophy is associated with increased diversification was recovered for both lineages while complex fruiting bodies and hymenophores were found to increase diversification only in the order Cantharellales.

VITA

Joshua Mark Birkebak was born in Burien, Washington (just outside of Seattle) on September 11th, 1989. From a very young age his parents could not get him to stop exploring the natural world around him. Through his homeschooling every trip to the park, beach, or mountains doubled as a field trip in natural history. He became enamored with mycology at middle school age and never quit pursuing a career in mycology. He received an Associates of Science from Highline Community College in Des Moines, WA in 2007 and subsequently transferred to the University of Washington in Seattle, WA. He graduated from the University of Washington in 2009 with a Bachelors degree in Biology: Plant Science where he also volunteered in the fungal herbarium and did undergraduate research in Mycology, Plant Pathology, and Palynology. He then came to the University of Tennessee to pursue a degree in Ecology and Evolutionary Biology specializing in mycology and molecular phylogenetics.